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ECOLOGICAL AND SYSTEMATIC STUDIES ON NORTH CAROLINA MYRIAPODS

by

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ECOLOGICAL AND SYSTEMATIC STUDIES ON NORTH CAROLINA MYRIAPODS

INTRODUCTION

With the exceptions of arctic, antarctic, and desert regions myriapods are distributed over all of the land areas of the earth. They usually inhabit dark, moist niches in almost every decaying log, every heap of leaf litter or pile of stones, and many cultivated fields. Such habitats provide two requirements which all myriapods have in common, protection from desiccation and a source of food.

In the past myriapods were generally regarded as of little or no economic importance, and zoologists confined their studies of them largely to morphological details of museum specimens. With the rise of ecology as a well defined branch of zoology, interest has shifted somewhat from descriptive morphology to living organisms. Considered from such a viewpoint, myriapods are not isolated specimens but members of complex soil communities in which many interacting forces are at work. Many species are important economically because of the part that they play in soil formation by helping transform dead leaves into humus.

This study is a contribution toward an understanding of certain aspects of the ecology and taxonomy of the myriapods of North Carolina. Whether ecology be defined as the science

of communities (Shelford 1929) or as the science of relationships of organisms to environment (Haeckel 1866), myriapods are excellent material for ecological studies. There are many interesting problems concerning their distribution, ranges of toleration, habitats, reproduction, feeding, and behavior.

I have employed the following methods in investigating the ecology and taxonomy of North Carolina myriapods: (1) collections were made in representative sections of North Carolina in order to determine the distribution of species; (2) a quadrat study was made of the distribution of myriapods in the principal plant-cover types in the Duke Forest; (3) specimens of several species were observed over a period of several months in cultures in the Duke Forest; (4) the desiccation of specimens of several species under varied humidities was determined; and (5) a study was made of the life history and habits of a representative millipede, Orthomorpha gracilis.

REVIEW OF LITERATURE

A Historical Survey of the Classification of Myriapods

For many centuries myriapods were designated, along with other small, creeping, legged animals, as Insecta. Writers from Aristotle to Linnè referred to all myriapods as either Julus (=Diplopoda) or Scolopendra (=Chilopoda). Aldrovandus (1602) designated them as Terrestria Aptera Multipeda and showed woodcuts of some (Wilson and Doner 1937). In the first edition of Systema Naturae Linnè (1735) referred myriapods, without specific names, to Ordo Insecta Aptera. The myriapods which were listed in the thirteenth edition of Systema Naturae (1806) were fourteen species of the genus Julus and thirteen species of the genus Scolopendra. One of these Scolopendrae is the annelid now known as Nereis mariana and another is a millipede.

After zoologists began making careful comparative anatomical studies in the late eighteenth century, old unnatural animal groups were slowly abandoned in favor of those that seemed to be more natural. Latzel (1880) summarized the various ideas concerning the relationships of myriapods and other animals as follows: "Nach Linnè's Vorgang sehen wir sie im vorigen Jahrhundert und zu Beginn dieses Jahrhunderts mit Flöhen, Läusen, ungeflügelten Wanzen, Springschwänzen, Zuchergästen, Scorpionen,

Spinnen, Zecken, Asseln, Krebsen u.s.w. in derselben Ordnung oder Klasse vereinigt." The present conception that myriapods represent four well defined classes of the Phylum Arthropoda was reached late in the nineteenth century.

Latreille first used the name Myriapoda in 1796; he designated the group as an order of Insecta and in it included present day terrestrial isopods and myriapods. In 1832 he raised Myriapoda to the rank of class, but there had been many changes suggested by others before then.

In 1800 Cuvier divided the heterogeneous group long known as Insecta into the classes Insecta and Crustacea; he included myriapods as an order in the former group. The following year Lamarck (1801) unfortunately included the present day arachnids and myriapods together in his Class Arachnida. They were separated by Leach (1814), who made Class Myriapoda equivalent to the three earlier established Classes Insecta, Crustacea, and Arachnida. Class Myriapoda was not generally recognized until 1837; even Leach himself gave it up and grouped the myriapods with crustaceans (Attems 1926).

None of the four distinct groups of myriapods were scientifically recognized until 1802 when Latreille divided his Subclass Myriapoda into Order Chilognatha (=Diplopoda) and Order Syngnatha (=Chilopoda). Recognition of the other two groups of myriapods came much more slowly. The genus Scolopendrella, known since 1761, was placed by most writers with the Chilopoda (Gervais 1844, Newport 1845), by a few with the Chilognatha

(Wood-Mason 1883), and by some with the Order Thysanura (Packard 1881a, 1883b). Ryder (1880, 1881a) designated the group as Symphyla and separated it from insects and other myriapods. Lubbock (1866) described the genus Pauropus and emphasized its isolation from previously described myriapods. The Class Myriapoda was divided (Latzel 1880) into three orders: Chilopoda, Symphyla, and Diplopoda, with Heterognatha as a suborder of Diplopoda. Later (Latzel 1884) the name Heterognatha was changed to Pauropoda, and that group was designated as the fourth order of Class Myriapoda.

Brandt (1841) separated myriapods on the basis of the position of the apertures of the genital organs into Opisthogoneata and Progoneata. This division was widely followed (Verhoeff 1902-1939, Attems 1930), but it has lately been rejected (Snodgrass 1938) as an all important criterion upon which to base relationships in favor of morphology of mouth parts and appendages and absence or presence of fused somites.

The Cuvierian idea of a distinct myriapod type was described (Wood 1869, p.138) as follows:

> [A] typical myriapodal segment is formed from two subsegements, each of which is originally . . . furnished with a single pair of appendages. The existent myriapodal segments follow two structural . . . modifications of the typical or ideal. . . . [In the Chilopoda] the anterior subsegment is so atrophied that it really forms no part of the perfected whole. Its appendages are entirely lost. . . . [The] posterior subsegment, with its appendages, is developed to the highest degree. . . . In the Diplopoda one subsegment is not thus developed at the expense of the other, but, the two coalescing, the perfected whole is obtained by their mutual growth.

Cuvier's idea of fixed types was abandoned long since in favor of the theory of common descent and blood relationship of all animals. Two men (Pocock 1887, Kingsley 1888) each came to the conclusion that there was no fixed myriapod type, that myriapods did not form a natural group, and that the possession of more than four pairs of legs was not sufficient basis for grouping animals together. Pocock (1893, 1897) offered the following system for Arthropoda Tracheata:

- Progoneata
    - Class Pauropoda
    - Class Symphyla
    - Class Diplopoda
- Opisthogoneata
    - Class Chilopoda
    - Class Insecta

This division of the old Class Myriapoda has been rather generally accepted. Hansen (1930), however, refused to abandon Myriapoda, and maintained, from a long study of arthropod mouth parts that the four groups of myriapods are more closely related to each other than many orders of Insecta are. But with most zoologists the name Myriapoda has lost taxonomic significance; it remains only as a convenient term for designating the Chilopoda and Progoneata.

1. Class Symphyla

The first symphylan species was described by Scopoli in 1761 as a member of the genus Scolopendra. The second species was called Geophilus junior by Gervais in 1836; he recognized

it as a distinct genus in 1839 and named it Scolopendrella. The most common and widely distributed species of the group, Scolopendrella immaculata, was described by Newport in 1844. He created for it a new family, which he put between the Lithobiidae and Scolopendridae, and emphasized the relationship with the former. In 1851 Menge pointed out that Scolopendrella is very much like Campodea in character and life habits, so it should be considered a transitional genus between the insect family Lepismidae and Scolopendridae (Michelbacher 1938).

Ryder (1880, 1881a) was the first who realized that these minute animals possessed characters distinct enough for them to be put in a separate order; he did not designate the class in which he believed it should be included, but he named the order "symphyla, in reference to the singular combination of myriapodous, insectean, and thysanurous characters which it represents."

Several theories were presented which were concerned with the position of symphylans with regard to other arthropods. According to the most widely accepted of these theories myriapods and insects were derived from a symphylan ancestry (Packard 1873; Haase 1886, 1889; Pocock 1893, 1897; Carpenter 1903, 1905; Crampton 1918; Calman 1936; Imms 1936). A similar theory was that protosymphlans, which arose from protomyriapods, gave rise to diplopods, pauropods, symphylans, and hexapods (Snodgrass 1938). According to a quite different theory, symphylans arose from insects and formed a transition between insects and myriapods (Hansen 1897; Silvestri 1901; Tillyard 1935). Symphylans

were thought by some to be in a suborder of thysanurans (Packard 1881a), of diplopods (Wood-Mason 1883), between pauropods and diplopods (Schmidt 1895), or that they formed a group by themselves (Ryder 1880, Latzel 1884, Packard 1903, and recent writers).

The number of described species of symphylans was only five until Hansen (1903) added 19. Bagnall (1913) named at least 21 others. The 54 species now known throughout the world represent three families and 10 or 12 genera (Attems 1926, Michelbacher 1938).

The best general work on the group was written by Verhoeff (1934), but he overlooked many important publications that are concerned with economic phases of symphylans.

2. Class Pauropoda

It is significant that Sir John Lubbock (1866), who first described the genus Pauropus, realized the importance of this newly discovered group. He stated that these animals "must certainly constitute a new family, Pauropodidae, and, I think, even a new order, which might be called Pauropoda." His valuable paper included descriptions and figures of two species of Pauropus, a description of the youngest larvae, mention of other larval forms, and biological observations.

As Order Heterognatha this group was regarded for a time as equivalent to Orders Chilognatha and Chilopoda (Humbert and Saussure 1872); however, in Latzel's (1880) system Pauropoda

appeared in the following position:

Class Myriapoda
  Order 1. Chilopoda
  Order 2. Symphyla
  Order 3. Diplopoda
    Suborder 1. Chilognatha
    Suborder 2. Colobognatha
    Suborder 3. Heterognatha (=Pauropoda)
  Order 4. Malacopoda (Family Peripatidae)

Later (Latzel 1884) the name Heterognatha was changed to Pauropoda; that group was designated as the fourth order of Class Myriapoda, and two families, Pauropoda agilia and Pauropoda tardigrada, were specified.

Monopoda (=Pauropoda) and Diplopoda constituted the only subclasses of Class Myriapoda in Bollman's (1893) system. Like Lubbock, this author considered the genera Pauropus and Polyxenus to be closely related. The two groups that they represented were later united by one author (Kenyon 1895) as Order Protodiplopoda. When the old Class Myriapoda was abandoned (Pocock 1897) Pauropoda was recognized as a class of Progoneata equivalent to Classes Symphyla and Diplopoda.

The three families recognized at the present time are composed of at least seven genera and more than 50 species.

Papers on anatomy and morphology of Pauropoda (Schmidt 1895, Kenyon 1895, Attems 1930, Verhoeff 1934) are far-outnumbered by papers which are essentially descriptions of species (Tömösvary 1884; Haase 1885; Daday 1889; Silvestri 1894, 1902; Kenyon 1895; Cook 1896c; Hansen 1901, 1917; Bagnall 1913; Harrison 1914;

[illegible]

[illegible]

[illegible]

[illegible]

Hilton 1928-1934). The most outstanding papers were by Lubbock (1868), Latzel (1884), Kenyon (1895), Hansen (1917), Attems (1926), and Verhoeff (1934).

3. Class Diplopoda

Before Latreille (1802) erected the Family Chilognatha (=Class Diplopoda) diplopods were lumped into a single genus, Julus, in the heterogeneous lot of animals designated by Linnè (1735-1768) as Ordo Insecta Aptera. Later Latreille (1806) set up the Class Myriapoda and included in it diplopods as Order Chilognatha, centipedes as Order Syngnatha, and terrestrial isopods as the third order.

Nine years later (Leach 1815) the recognized families and genera of the Order Chilognatha were as follows:

Family Glomerides: Glomeris
Family Julides: Julus, Craspedosoma
Family Polydesmides: Polydesmus

The following system (Brandt 1841) represented a great advance in the knowledge of diplopods:

- Order Chilognatha of Class Hexapoda
  - Suborder Myriapoda Sugentia (=millipedes with mouth parts adapted for sucking)
  - Suborder Myriapoda Manducantia
    - Tribe Chilopoda (=centipedes)
    - Tribe Chilognatha (=millipedes with mouth parts adapted for chewing)
      - a. Monozonia: Polyxenus, Polydesmus, Strongylosoma
      - b. Trizonia: Julus, Spirobolus, Lysiopetalum, etc.
      - c. Pentazonia: Glomeris, Sphaerotherium, Sphaeropoeus.

These two suborders showed Brandt's failure to recognize the fact that diplopods form a natural group, but his arrangement of the Tribe Chilognatha still deserves recognition because he based it upon important morphological characteristics which had not been observed before.

The isolated position of Brandt's Suborder Sugentia was realized by Newport (1844), and he abandoned that division; he erroneously put the genera previously included in Sugentia with the Julidae. His change, however, is significant because he was the first who had a concept of the diplopods as a uniform group. His division of the Order Chilognatha into the following tribes is not as good as Brandt's:

I. Pentazonia: Glomeridae
II. Bizonia: Iulidae, Polyzonidae, Siphonophoridae
III. Monozonia: Polyxenidae, Polydesmidae

Other divisions of the diplopods were made (Gervais 1844, C. L. Koch 1847, Wood 1869) within the next few years, but the authors of all of them failed to discover the correct relationship because they confused structural adaptations with fundamental morphological differences. A fairly good idea of natural relationships was given by Saussure and Humbert (1872) in the following system:

I. Suborder with the Glomeridae
II. Suborder with the Polyxenidae
III. Suborder with the Craspedosomidae, Polyzonidae, and Julidae

Latzel (1884) showed the importance of gonopods for the characterization of species of diplopods and made the following division:

Class Myriapoda
   Suborder Pselaphognatha: Polyxenidae
   Suborder Chilognatha: Glomeridae, Polydesmidae, Chordeumidae, Iulidae
   Suborder Colobognatha: Polyzonidae

The system of Pocock (1887, 1893) was more like those of present day writers than any earlier ones:

Class Diplopoda
   Subclass Pselaphognatha
   Subclass Chilognatha
      Order Oniscomorpha
      Order Helminthomorpha
      Order Limacomorpha

Bollman's (1893) system was similar except that he retained Diplopoda as a subclass of Class Myriapoda and substituted the name Podochila for Pselaphognatha.

The termsOpisthandria and Proterandria were introduced (Verhoeff 1894) to designate the groups of diplopods in which the copulatory legs of the male are located at the posterior part of the body from the group in which they are located on the seventh or the eighth post-cephalic somite. This latter group, Proterandria (=Helminthomorpha), was divided (Attems 1898) into Eugnatha and Colobognatha on the basis of the structure of mouth parts.

The following system of classification was advanced by Cook in 1895 and modified in 1899:

- Class Diplopoda
  - Order Oniscomorpha
  - Order Merocheta: Polydesmoidea
  - Order Colobognatha
  - Order Anocheta: Spiroboloidea
  - Order Zygocheta
  - Order Coleocheta: Lysiopetaloidea, Chordeumoidea, Strierioidea
  - Order Diplocheta

The most significant feature of this system was the prominent place given the Coleocheta, the group later known as Nematophora (Verhoeff 1928).

The systems of classification of diplopoda published most recently (Attems 1930, Verhoeff 1928) are basically similer, although they differ somewhat in terminology. Their greatest difference is in the rank of the Colobognatha. The division of Class Diplopoda by Attems (1930) is as follows:

- Subclass Pselaphognatha
- Subclass Chilognatha
  - Division Opisthandria
    - Order Limacomorpha
    - Order Oniscomorpha
      - Suborder Sphaerotheria
      - Suborder Glomeridea
  - Division Proterandria
    - Superorder Eugnatha
      - Order Polydesmoidea
        - Suborder Polydesmidea
        - Suborder Strongylosomidea
      - Order Nematophora
        - Suborder Chordeumoidea
        - Suborder Stemmiuloidea
      - Order Juliformia
        - Suborder Juloidea
        - Suborder Spiroboloidea
        - Suborder Spirostreptomorpha
          - Subsuborder Spirostreptoidea
          - Subsuborder Cambaloidea
    - Superorder Colobognatha

Verhoeff (1928) made the following division of the Class Diplopoda:

- Subclass Pselaphognatha
  - Order Schizocephala
- Subclass Chilognatha
  - Superorder Opisthandria
    - Order Limacomorpha
    - Order Armadillomorpha
  - Superorder Proterandria
    - Order Colobognatha
    - Order Nematomorpha
    - Order Proterospermophora
      - Suborder Polydesmoidea
    - Order Opistospermophora
      - Regim. Symphyognatha
        - Suborder Iuloidea
      - Regim. Chorizognatha
        - Suborder Spiroboloidea
        - Suborder Spirostreptoidea
        - Suborder Cambaloidea

More than 900 genera and several thousand species of diplopods have been described. For many years Latzel's (1884) work was the most comprehensive that had been published. The recent works of Attems (1930) and Verhoeff (1928) include taxonomic descriptions as far as genera. The most outstanding monograph is on the Polydesmoidea (Attems 1898-1899, 1938).

4. Class Chilopoda

Like diplopods, chilopods also were lumped into a single genus, Scolopendra, by Linnè. Latrielle (1802) first designated chilopods as Syngnatha, but he later (1817) changed the name to Chilopoda and gave the group the rank of family in the Order Myriapoda of the Class Insecta.

The commonest genera were described and arranged in the following families by Leach (1814):

Order Syngnatha
  Family Cermatides: Cermatia
  Family Scolopendrides: Lithobius, Scolopendra, Cryptops
  Family Geophilides: Geophilus

The groups of chilopods that form the basis for even the latest systems of classification were early set up as the families Scutigeridae (Cermatiidae), Lithobiidae, Scolopendridae, and Geophilidae (Newport 1844). There can be little difference of opinion about these as distinct groups, but there have been disputes over their mutual relations and over the relations of the animals within each group.

The number of body somites (Meinert 1870) and the presence or absence of larval forms were important criteria emphasized in the following system (Haase 1880):

I. Suborder Chilopoda Anamorpha: 15 body somites
  Family Scutigerini
  Family Lithobiini
II. Suborder Chilopoda Epimorpha: 21 or more body somites
  Family Scolopendridae
  Family Geophilidae

Latzel (1880) followed Newport's (1844) division in his excellent volume that remained the best morphological work on chilopods for many years.

Bollman (1893) wrote: "In accordance with the views recently advanced by Pocock, Kingsley, and several continental writers, I have regarded the Syngnatha as being more closely allied to the Hexapoda than to any orders of the old group of Myriapoda." He made the following division of Syngnatha (=Chilopoda).

Class Etymochila
    Subclass I. Syngnatha
        Order I. Anamorpha
            Suborder I. Unguipalpi
                Family I. Lithobiidae
                Family II. Cermatobiidae
            Suborder II. Schizotarsia
                Family III. Scutigeridae
        Order II. Epimorpha
                Family IV. Scolopendridae
                Family V. Geophilidae
    Subclass II. Hexapoda

Pocock (1902) based his division of larger groups on the location of spiracles. The weakest part of his system, which is given below, was the omission of Haase's divisions Anamorpha and Epimorpha.

Class Chilopoda
    Subclass Pleurostigma
        Order Geophilomorpha
        Order Scolopendromorpha
        Order Craterostigmorphora (Scutigeromorpha)
    Subclass Notostigma
        Order Scutigeromorpha

Verhoeff (1925) combined ideas from both Haase (1880) and Pocock when he set up the following system of chilopod classification:

Subclass I. Notostigmorphora
    Family Scutigeridae
Subclass II. Pleurostigmorphora
    Order I. Anamorpha
        Suborder I. Craterostigmorphora
        Suborder II. Lithobiomorpha
    Order II. Epimorpha
        Suborder I. Scolopendromorpha
        Suborder II. Geophilomorpha

The following separation of the distinct chilopod groups by Attems (1930) is similar to that of Haase (1880):

Subclass Epimorpha
  Order Geophilomorpha
  Order Scolopendromorpha
Subclass Anamorpha
  Order Lithobiomorpha
  Order Scutigeromorpha

Important investigations that led to a more nearly natural arrangement of smaller taxonomic groups were made by: Heymons (1901) on the development of Scolopendra, Krepelin (1903) on the revision of Scolopendridae, Attems (1903, 1909) on the systematics of the Geophilidae, Verhoeff (1904-1905) on the systematics of the Himanteriidae, and Brölemann and Ribaut (1912) on Schendylina. Investigations by American writers will be mentioned in the section concerned with the literature on myriapods of the United States.

The Ecology of Myriapods

The literature dealing with the ecology of myriapods is both fragmentary and scattered. Verhoeff (1925, 1928, 1932, 1934) brought much of it together in four volumes of Bronns Klassen und Ordnungen des Tier-Reich. Attems' (1930) sections on ecology in Kukenthals Handbuch der Zoologie are good, but very brief. Both of these authors treated more of morphology and taxonomy than of ecology.

The best accounts of the ecology of Symphyla are in the writings of Verhoeff (1934), Friedel (1928), and Michelbacher (1938). Numerous papers have been published (Michelbacher 1938, p.109) dealing with the habits of the symphylan, Scutigerella

immaculata, which is often a serious pest on cultivated plants.

Symphylans are scattered over most of the world, with the exception of north of 63° lat. N. in Europe and Asia and 48° lat. N. in North America, where their distribution is limited by a minimum temperature of 15° C (Michelbacher 1938). They have been found at all altitudes between 3,000 meters (Friedel 1928) and sea level.

Symphylans were once reported to occur solely in shaded rocky soil (Grassi 1886), but they are known to be numerous in moist, cool soil and humus and under logs in woods, gardens, and fields (Newport 1845, Menge 1851, Muhr 1881, Latzel 1884, Williams 1907). Although absent from most caves (Verhoef 1934) they do occur in some under bat droppings (Joseph 1882). Occasionally they occur in ant nests (Evans 1909).

The chief ecological factor that influences the horizontal and vertical distribution of symphylans is the moisture of the soil and of the soil air (Friedel 1928). Other important factors are: location, vegetation, soil texture and structure, soil temperature, manuring of soil, and natural enemies (Michelbacher 1938). Vertical migrations, which may be from three to five feet down into the soil, may be in search of a depth where the optimum temperature, 65° F (Filinger 1931) or between 50° F and 60° F (Miles and Cohen 1935), obtains; more likely, migrations are complicated reactions to the following several factors rather than to one factor: temperature, moisture, food, soil texture, and soil structure (Michelbacher 1938).

The structure of mouth parts, the straight digestive tract, and fast movements were early taken as evidence that symphylans were predacious (Newport 1845, Latzel 1884). Later, symphylans were reported to feed partly (Williams 1907) or entirely (Thompson 1924) on humus. They are known to feed also on living tissues of cultivated plants (Riley 1929, Filinger 1931), on compressed yeast, unicellular green algae, their own dead and injured, and fungal growth or humus in laboratory cultures (Michelbacher 1938). Verhoeff (1934) observed no predacious habits, nor did a study of mouth parts lead him to believe that symphylans were predacious.

Since attention was first called to the damage that certain symphylans do to growing crops these animals have been reported attacking many different kinds of plants, generally the roots, throughout the world (Michelbacher 1938). One square meter of favorable forest soil may contain 50 symphylans (Friedel 1928), while an area of the same size in infested fields may yield from 1,250 to 10,760 (Michelbacher 1938). The most suitable control measure in fields is flooding (Essig 1915); steam, fumigants, and poison baits are used with varying degrees of effectiveness in greenhouses (Michelbacher 1938).

Centipedes and larvae and adults of at least two species of beetles feed on symphylans (Menge 1851; Filinger 1928, 1931; Illingworth 1927, 1928; Wymore 1931; Michelbacher 1938). Gamasid mites may attack symphylans (Wymore 1931), but there is no evidence of it except that they commonly occur in the same habitats

(Michelbacher 1938). Hundreds of tyroglypid nymphs have been observed riding about on Scutigerella immaculata, apparently without doing any damage (Michelbacher 1938). Sporozoans have been reported from the midgut of the same species (Verhoeff, 1934).

The optimum temperature for normal activities of Scutigerella immaculata, according to Michelbacher (1938), is between 12° C and 20° C. The animals that he studied molted most frequently at a temperature of 26° C. They survived a temperature of 2° C for long periods but were unable to withstand 0° C for any length of time. At 28° C some individuals laid eggs between the seventh and eighth molts; at 21° C the first eggs were obtained between the ninth and tenth molts.

Symphylans are negatively phototrophic, but it is not uncommon for members of at least one species, Scutigerella immaculata, to come to the surface of the soil and feed or even lie there motionless during the day (Michelbacher 1938).

There is not a single ecological work on the Pauropoda; their small size and secluded mode of living makes them very difficult to collect and to study. They have been reported in Europe, as far north as 60° latitude, in Asia, Australia, North and South America, and Siam at altitudes ranging from sea level to more than 2000 meters. Their favorite habitat is under stones in dense woods, but they also occur under rotting logs, leaf litter, and lumps of clay (Hansen 1901; Hilton 1928, 1930).

Slowly moving pauropods probably eat decomposing remains of animals and plants and the swiftly moving species eat microscopic animals (Latzel 1884). One species was found feeding on dead dipterans floating on the surface of a puddle (Verhoeff 1934).

The most general discussions of the biology of the Diplopoda were written by vom Rath (1891), Chalande (1905), Attems (1930), and Verhoeff (1928). As with other groups of myriapods, this phase of diplopods has been discussed far less than morphology and taxonomy.

Diplopods are seldom specialists as to habitat, but some species show a preference for certain habitats. The seventeen "topobiologischen" groups which Verhoeff (1928) found among middle European diplopods occurred in the following habitats: forest soil, lowland forests, sand, bark, humus, steppes, subterranean cavities, lower mountains, highest mountains, caverns, sea coast, inland streams, ant and termite nests, mole burrows, regions rich in limestone, and fern beds. Attems (1930) believed that diplopods might be grouped as animals of woods, stony soil, fields, steppes, bark, caverns, and highest mountains.

The appearance of different stages and activities in the life cycle of diplopods is closely related to seasonal changes. Certain European species that mature in one year in the lowlands require two years to reach maturity in the mountains and three years in the highest mountains (Verhoeff 1928).

Either larvae or adults hibernate in crevices in the ground or in chambers prepared by themselves. Similar chambers serve as

protection during moulting, dry seasons, and winter cold. Several authors (vom Rath 1891, Rossi 1901, Evans 1910, Voges 1916, Heymons 1915, and Verhoeff 1928) described the building of these chambers; none agreed on all the details of construction.

Diplopods, in general, remain more active during cold weather than most insects do. Conotyla fischeri was found moving about on an ice covered log when beetles and spiders under the log were too chilled to move (Cook 1912). Orobainosoma fonticulorum was seen copulating on snow (Chamberlin 1930). Diplopods recovered after being frozen in blocks of ice if they were thawed out slowly (Morgan 1939). Specimens of Underwoodia polygama, if held in the hand and exposed to sunlight, "were soon able to run in the ordinary way, wriggled convulsively a few times and died"(Cook 1912). Locomotion of Parajulus pennsylvanicus became obviously irregular below 15° C; the rate of progression was practically constant at temperatures between 15° and 30° C (Crozier 1924).

Cylindroiulus londinensis, C. meinerti, and Blaniulus guttulatus have a "feuchtigkeitssinn" (Verhoeff 1928). Experimental animals of these species preferred a moist light place rather than a dark dry place. The fact that diplopods occurred in trees only on very foggy days led Verhoeff to believe that the chief factor that causes diplopods to remain in the soil is humidity and not a negative phototropism.

Plateau (1887) described the behavior of myriapods toward light, and it was his work that Radl (1901) quoted. Müller (1924) studied the light reaction of Iulus fallax and Polydesmus complanatus. In the first species, which has ocelli, he could find

no evidence of photodermic sense organs, while in the second species, which has no ocelli, he found a light sensitive organ on the antennae and evidence for the presence of a photodermic sense. Other writers (Fabre 1855, vom Rath 1890 and 1891, Clementi 1912, Lohner 1914, Verhoeff 1896-1928) discussed the reactions of diplopods toward light, but none did it so carefully or so thoroughly as Müller.

Several authors referred to the increased activities of diplopods during the night. Park (1935) studied the nocturnal movements of Spirobolus marginatus. He wrote: "Of a total of 432 hours spent in a dark experimental chamber, roughly 88 per cent of the activity of the starving animal was at night, and 8.5 per cent during the day. Hence we are led to believe that their inate activity is a deep-seated mechanism."

Parental care varies greatly among diplopods and consists, in so far as is known, only in construction of nests and care of eggs. The most intimate care is given by females in the Suborder Colobognatha; they wrap their bodies around the clutches of eggs and give off unusually large amounts of secretion from the repugnatorial glands during the incubation period. Eggs of Polyxenus lagurus are deposited in clutches of from 10 to 20; they adhere together and are covered loosely by trichomes from the female's body. Among the Craspedosomidae, females construct egg cocoons of white webs from the secretion of the posterior spinning glands and leave them in crevices in the earth. The eggs of Glomeris (Verhoeff 1928) and Spirobolus (Loomis 1933), which are quite unrelated genera, are deposited singly and enclosed in capsules composed of soil and secretions from anal

glands. Many polydesmids and some julids construct egg chambers of earth or soft wood passed through the gut or moistened with salivary juices and shaped with the jaws and front feet. These chambers are dome-like or chimney-shaped (Verhoeff 1928).

Latzel (1884), vom Rath (1891), Attems (1894), Morse (1904), Evans (1910), Barber (1915a), Verhoeff (1916, 1928), Muller (1924), Miley (1927a), and Loomis (1933) studied breeding habits of diplopods, chiefly polydesmids and julids.

Diplopods feed chiefly on decaying plant material. Although members of certain species show a preference for one type of humus over another, there are no food specialists as among insects. In general, humus from hardwood trees is preferred over that from coniferous tress, and certain hardwoods, notably maple, hazelnut, and alder, are preferred over others. Species of glomerids which live in open areas must swallow sand grains to grind their hard food particles, but those which eat only very soft food rarely take in sand (Verhoeff 1914, 1928). Blaniulus guttulatus is reported to feed on human excreta, bodies of dead animals, and agricultural crops (Thomas 1904). Other julids are known to prefer the flesh of dead animals to vegetable matter (Krause 1920, Verhoeff 1928). A cave-dwelling lysiopetalid captures and eats living earthworms and spiders (Verhoeff 1928). "Pseudoparasitism," or the presence of diplopods in the digestive tract and nasal passages, of human beings occurs occasionally; such infections are accidental and doubtless many reports of them are ficticious or greatly exaggerated (Blanchard 1902, 1910; Chamberlin 1923a). Members of the genus Macheiriophoron are chiefly fungus eaters (Verhoeff 1928).

It is not unusual for diplopods, chiefly julids, to feed on cultivated plants, either on dead parts or on living tissues (Fitch 1865, Walsh 1866, Coquillett 1882, Forbes 1884, Theobald 1903, Cook 1911a, Essig 1915, Riley and Johannsen 1932).

It is a recognized fact that earthworms have no monopoly in mull formation, but that diplopods may also play a significant role in the destruction of leaf litter (Latzel 1884, Hoffman 1931) and the mixing of mineral soil and humus (Plateau 1876, Coville 1914). Members of some species, notably *Fontaria trimaculata* and *F. coriacea*, ingest large amounts of humus and some soil (Romell 1935). A plot 4 by 20 feet in a wooded area near Washington, D. C., yielded 320 specimens of *Spirobolus marginatus*, the adults of which produced about 0.5 cc of excreta per day. On an acre with the same population density this species would contribute to the formation of more than two tons of leaf mold each year (Coville 1913). This amount is spectacular rather than significant; diplopods do aggregate where favorable feeding sites are located, but rarely in such a large plot as Coville described. Wolcott (1937) considered the significance of millipedes in an environment to be slight. In one hundred square feet of grassland he found more than 600 millipedes, roughly ten per cent of the total number of animals present on that area; one-half of them were on the surface, one-fourth in the top two inches of soil, and the remainder were as much as eight inches from the surface.

Very little is known about the parasites of diplopods. Gregarines (vom Rath 1891, Wilson 1915, Attems 1930) and sporozoa

(Labbè 1899) occur in the digestive tract; dipterous larvae and nematodes are often present in the body cavity (Haase 1885, vom Rath 1891, Barber 1915, Verhoeff 1928). Mites are frequent ectoparasites; they attack eggs and larvae, as well as adults (Verhoeff 1928). Parasitic fungi often attack diplopods, usually at the soft limb joints; infection probably occurs during molting when the exoskeleton is soft (Shellenberg 1923).

Some insects, spiders, and insectivorous vertebrates, especially toads, frogs, salamanders, lizards, birds, field mice, and moles, are natural enemies of diplopods (Verhoeff 1928). It is reported that twelve per cent of the diet of the American toad consists of diplopods (Kirkland, 1897, 1904).

Means of protection are varied among diplopods. Polyxenus has a thick covering of trichomes; many species have exoskeletons heavily impregnated with calcium; the spiral reflex is well developed in species with round, smooth bodies. Somediplopods give off secretions from repugnatorial and rectal glands that are avoided by many animals (Verhoeff 1928). Certain beetle larvae, however, eat the repugnatorial secretions. An unusual diplopod in Hispaniola has the ability of ejecting its repugnatorial secretions far from the body; its secretions, unlike those of most other diplopods, are a painful irritant to the human skin (Loomis 1936).

Myrmecophilous and termitophilous species of diplopods have been described (Verhoeff 1891, Silvestri 1911a, Chamberlin 1923d, Schubert 1939). The not infrequent occurrence of diplopods in mole burrows is probably fortuitous (Silvestri 1911, Heselhaus

1914, Schubert 1939). A symbiotic relationship between a julid and earthworms, and relationships of uncertain classification, but probably commensal or symbiotic, between diplopods and aphids and diplopods and insect larvae have been reported (Verhoeff 1928). Diplopods also occur in hornet, bumblebee, and bird nests. In general, the species found in animal nests are those with a wide range of habitat (Schubert 1939).

An unusual abundance of diplopods was referred to by various authors as "swarmings" (Mauch 1901, Cook 1924), "migrating armies" (Barber 1915), "perambulating millipeds" (Viosca 1925), "over-population"(Verhoeff 1900), and "migration" (Sinclair 1922 and Heape 1921). Mass movements of the following species have been reported: Brachyiulus unilineatus (J. Paszlovszky 1879), Fontaria virginensis (Bollman 1893, Mauch 1901), Julus terrestris and Brachyjulus sp. (Verhoeff 1900), Parajulus pennsylvanicus (Morse 1903), Chonaphe sp. (Barber 1915), Tachypodoiulus niger and Cylindroiulus londinensis, var. coeruleocinctus (Brade-Birks 1922), Spirostreptus sp. (Cook 1924), and Spirobolus marginatus (Viosca 1925).

The distribution of diplopods in the five great geographical regions of the world indicates that the large species characteristic of the tropics and the smaller types characteristic of holarctic regions are expressions of present climatic conditions. Diplopods, because of their intolerance to water and narrow range, may be better indicators of former land areas and bridges than terrestrial molluscs (Attems 1930).

The following are characteristic habitats of chilopods:

forest soil, under bark, borders of streams, sea coasts, stony soil, soft soil, sand, high mountains, caverns, and subterranean crevices; few species are confined to a single type of habitat. Some of the Lithobiidae found in caverns are marked by a decrease in the number of ocelli, an increase in the length of antennae, and an absence of pigment (Verhoeff 1925). Blind chilopods also occur outside of caverns.

The type of food differs somewhat among the four main groups of chilopods, but all of them are carnivorous. Lithobiidae eat flies, mosquitoes, beetles, other insects, spiders, and soft vegetable matter (Koch 1863, Plateau 1876, Britten 1920, and Verhoeff 1925). Scolopendridae (especially *Scolopendra cingulata* and *S. dalmatica*) prefer soft worms, larvae, and dead insects and only hunger drives them to taking moving insects (Heymons 1901). In a figure in Brehms *Tierleben* a Scolopendra is showed attacking a lizard as large as itself. Campbell (1932) gave a list of the insects that *Scolopendra heros* ate in captivity, but she did not state the number eaten. *Scutigera forceps* ate roaches, houses flies, moths, bedbugs, croton bugs, and spiders in captivity (Murtfedt 1894, Marlatt 1908, and Verhoeff 1925). All chilopods with fifteen segments, *i.e.* Lithobiidae and Scutigeridae, eat insects and usually avoid slimy worms and snails (Verhoeff 1925).

The chief enemies of chilopods are field mice, moles, lizards, ground-feeding birds, thysanurans, ants, scorpions, and ground spiders (Verhoeff 1925). Sporozoa (Labbé 1899), gregarines (Leger and Dubascq 1902 and Wilson 1915), nematodes (Balbiani 1889), and dipterous larvae (Tölg 1913) are parasitic on chilopods.

There are no records of chilopods that are parasitic on other plants or animals, but a "pseudoparasitism" of various geophilids, Lithobius forficatus, and Scutigera coleoptrata, in the nasal passages and digestive tracts of human beings has been reported (Blanchard 1898, 1902, 1910; Verdun et Brouyout 1912; Laurens 1914).

Copulation has not been observed with certainty in any chilopods, but it probably takes place among the Lithobiomorpha and the Scutigeromorpha. In the Geophilomorpha and Scolopendromorpha the males deposit spermatophores from which the females fertilize themselves. Lithobiids lay eggs singly, probably one or two daily. The female uses the gonopods and hind legs to roll the egg until it is covered with dust and then she abandons it. Female geophilids and scolopendras lay eggs in masses and coil around them during the incubation period. They usually stay with the young during the first three immature stages (Fabre 1855, Verhoeff 1928).

One Scolopendra (Brockhausen 1903) and several geophilids are luminescent. The luminescent substance first was thought to be secreted by the epithelium of the digestive tract (Dubois 1887, 1893) or by the anal and coxal glands (Mace 1886), but now it is thought to be secreted by the glands of the sternites and the pro- and metacoxae (Gazagnaire 1888, Haase 1889, Ludwig 1901, Brade-Birks 1920, Verhoeff 1925). The strength of the light emitted varies with the species, sex, individual, and season (Brade-Birks 1920). Bacteria, as well as the secretions of the glands mentioned above, are sometimes responsible for luminescence (Verhoeff 1925).

Records of mass movements of chilopods are rare. The most remarkable case was recorded by Aelian (Heape 1931), who stated that the whole population of the town of Rhetium was driven out by swarms of emigrating Scolopendrae. Thuringer (1924) also found many Scolopendrae migrating. Sinclair (1895, 1917) reported sudden increases in the numbers of geophilids and lithobids, which he attributed to extremely favorable reproductive conditions.

Chilopod species usually have a wider range than diplopod species; there are more arctic and antarctic species of chilopods than there are of diplopods (Verhoeff 1925, Attems 1930). Geophilomorpha and Lithobiomorpha are characteristic of temperate regions, and Scolopendromorpha and Scutigeromorpha of tropical regions (Verhoeff 1925).

Myriapods in the United States

The earliest published works on North American myriapods consisted largely of short papers scattered among scientific periodical literature in several languages. The chief European contributors were Rafinesque (1820), Brandt (1841), Newport (1844), C. L. Koch (1847, 1863), Girard (1853), Sager (1856), Humbert and Saussure (1869, 1872), Borre (1884), Gervais (1847), Karsch (1881, 1881a), Kohlrausch (1881), Latzel (1880, 1884), Meinert (1885), Pocock (1888), Provancher (1883), and Stuxberg (1875, 1877, 1885). Their work consisted almost entirely of descriptions of new species.

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Thomas Say was the first American who made a careful study of the myriapods of the United States. He (1821) described eighteen species, mostly from the Southern States. Wood (1861-1869) published a more extensive series of papers. In his "Myriapoda of North America" (1869) he included descriptions of the ninety-two species then known to be in the United States. Cope (1869, 1870, 1872), Packard (1873), and Ryder (1881) described several cave species.

Soon after Lubbock discovered Pauropus in Europe, Packard (1870a) and Ryder (1878, 1879, 1879a) reported related genera and species in the United States. Kenyon (1895) and Cook (1896c) wrote on the morphology and classification of pauropods.

Among the early publications that dealt with other phases of myriapods than morphology and classification were a few notes on some poisonous species, a description of the eyes and brain of Cermatia forceps (Packard 1880), brief notes on the habits of a few species (Wood 1863-1869), and references to the destructive habits of certain myriapods (Fitch 1865, Walsh 1866, Wood 1869, Coquillet 1882, and Forbes 1884).

In his summary of American myriapods Underwood (1885) listed 27 genera and 129 species. McNeill (1887, 1887a, 1888) added 19 others. The taxonomic work of C. L. Bollman, who died before he was twenty-one years old, was superior to that of any other American before him. His publications (1887-1893) showed evidence of keen observing powers and careful judgment combined with great enthusiasm and activity. He made careful descriptions of 63 new

species and three genera. His scientific writings on myriapods were collected by Underwood (1893), who included with them a review of literature published on North American myriapods before 1893.

A botanist, O. F. Cook, published several papers concerned with the taxonomy of American species. His most important papers dealt with the Geophilidae (1896a, Cook and Collins 1890), Craspedosomatidae (Cook and Loomis 1928). He was one of the few Americans who attempted to give explanations of myriapod evolution (1901, 1911), distribution (1911), and adaptations (Cook and Loomis 1924).

The foremost authority in the United States on the myriapod Classes Diplopoda and Chilopoda is Dr. R. V. Chamberlin. His most important publications are concerned with the morphology of species in the following groups: Lithobiomorpha (1911b, 1912, 1912b, 1913, 1916a, 1917a, 1922a, 1925b, 1925c), Geophilomorpha (1912e, 1920b), Julidae and Isobatidae (1921, 1940b) and Fontariidae (1918a, 1939). H. F. Loomis described new American species of the Order Colobognatha (1934) and of the Families Striariidae (1936a) and Lysiopetalidae (1937). New symphylans and pauropods were described by Hilton (1930-1934). Myriapods collected in caves in the Eastern States were listed by Dearolf (1937, 1938) and Loomis (1939).

"The Biology of the Garden Centipede, Scutigerella immaculata" (Michelbacher 1938) is the best ecological work on a myriapod that

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has been done in the United States. There have been briefer publications and references, in addition to those already mentioned in this section, to behavior (Williams 1907, Crozier and Moore 1923, Crozier 1924, Wymore 1931), evolution (Kingsley 1888; Packard 1903; Tothill 1916; Crampton 1918, 1928; Ewing 1928; Snodgrass 1938), distribution (Hilton 1930, Wymore 1931, Wolcott 1937), life histories (Barber 1915a, Miley 1927a, Hilton 1929, Hefner 1929, Wymore 1931, Campbell 1932, Loomis 1933, Cornwell 1934), mull formation (Coville 1914, Romell 1935), morphology (Hefner 1929a, Miley 1930, Hilton 1930a), predators (Kirkland 1897, 1904; Sweetman 1936), parasites (Barber 1915, Wilson 1915), and the control of myriapods that are pests on agricultural plants (see bibliography of Michelbacher 1938).

Bollman (1887) described three species of myriapods sent to him from North Carolina by Professor George F. Atkinson. The collection that M. Eugène Simon made in North Carolina was described by Brölemann (1896). Chamberlin collected thirteen previously undescribed species of Lithobiomorpha (1911b, 1913) and five of the Family Fontariidae (1939) in the western part of North Carolina during the summer of 1910. Since then he has described many species sent to him from that state by Dr. A. S. Pearse, Dr. C. S. Brimley, Mr. W. S. Cornwell, and myself. Brimley (1938) listed 68 species known to exist in North Carolina; my work brings the number to 96.

THE RELATIONSHIPS OF MYRIAPODS

The four distinct classes to which myriapods belong can be briefly described as follows:

Symphyla: antennae simple and multiarticulate; mandibles two-segmented and with movable lacinia; two pairs of maxillae; elongated body consists of a head and either fifteen or twenty-two post-cephalic somites; each somite bears a visible tergite; twelve pairs of legs, the first pair sometimes greatly reduced; spinning glands open on the well developed cerci on the last somite; median genital opening behind the third pair of legs on the fourth somite; one pair of spiracles ventral to antennae; anamorphic; larvae with 6, 7, 8, 9, 10, or 11 pairs of legs.

Pauropoda: antennae consists of four proximal segments and a pair of distal branches that bear three filaments; one pair of unsegmented mandibles; one pair of maxillae; body consists of a head and twelve post-cephalic somites; either six or ten tergites; nine pairs of functional legs; genital openings paired in male and single in female, posterior to the second pair of legs; respiratory and circulatory systems lacking; anamorphic; larvae with 3, 5, 6, 8 pairs of legs known.

Diplopoda: antennae simple, usually consist of eight segments; mandibles two-segmented and with movable lacinia; first

maxillae absent in adults; gnathochilarium formed from second maxillae and part of the first post-cephalic somite; body consists of an anterior region of single somites, the thorax, and a posterior region of fused or doubled somites, the abdomen; first somite of the thorax legless, the next three, occasionally four, somites bear one pair of legs each; the doubled somites of the abdomen bear two pairs of legs each; one pair of spiracles generally opens at the base of each pair of legs; paired genital openings on the third post-cephalic somite; anamorphic; larvae with three or more pairs of legs.

Chilopoda: antennae simple and multiarticulate; one pair of segmented mandibles; two pairs of maxillae; elongated body consists of a head and from 19 to almost 200 single post-cehpalic somites; each post-cepahlic somite except the first and the last three bears a pair of running legs; appendages of the first somites modified as poison claws; a single genital opening on the preanal somite; spiracles open on pleurites or on tergites; either anamorphic or epimorphic; larvae with seven or more pairs of legs.

According to a theory which Tillyard (1935) postulated, the myriapod-hexapod group of Arthropoda arose from an ancestor with only four post-cepahlic somites. He designated these somites as A, B, Y, and Z and assumed that A, B, and Y each bore one pair of legs, that the gonopores opened on somite Y, and that the anus opened on somite Z. Hexapods arose from a line in which anamorphoses were accompanied by subdivisions of somites Y and B; myriapods arose from another line in which such subdivisions

occurred in somite Y, never in somite B, and rarely in somite Z. In the progoneate types of myriapods "additional segments budded off from Y backwards, leaving the gonopores on the third segment. In Symphyla, it is suggested either that the fourth segment, having the gonopores, is the original segment Y (in which case B has divided into two) or that the gonopores have moved back one segment. The evidence seems to be mostly in favor of the latter. . . . In the Diplopoda the division of segments by anamorphosis has followed the same lines as the Pauropoda but has gone much further." In the opisthogoneate myriapods "the original genital segment Y has remained next to Z, the anamorphic additions being made in front of it." Tillyard (1936) did not give a figure to illustrate this theory, but his argument indicated to the author that he had the idea of myriapod relationships that is shown in Figure 1. He regarded the Pauropoda as the most primitive of the progoneate myriapods because of the small number of body somites and the lack of plates in the sternal and pleural regions.

Verhoeff (1925) and Attems (1930) followed Pocock (1893) in his belief that the location of the opening of the genital organs is of fundamental importance in working out the relationships of the classes of myriapods. Accordingly, they designated Symphyla, Pauropoda, and Diplopoda as Progoneata and Chilopoda and Hexapoda as Opisthogoneata and (Verhoeff 1925) gave the following as fundamental differences between the two groups:

Progoneata	Opisthogoneata
1. Middle portion of mandible strongly developed.	1. Middle portion of mandible weak or absent.
2. One pair of maxillae.	2. Two pairs of maxillae.
3. Anterior genital opening.	3. Posterior genital opening.
4. Gonopods usually present in male.	4. Gonopods absent or inconspicuous in male.
5. Skeleton often of chitin and calcareous material.	5. Skeleton of chitin.
6. Tracheae never anastomosing.	6. Tracheae anastomosing (except in Scutigera).

Verhoeff (1925) showed his ideas of the relationships of myriapods as is indicated in Figure 2. He believed that the Symphyla, Pauropoda, and Diplopoda have fundemental differences great enough to derive them from three separate lines of evolution from the ancestral progoneate stock.

Hansen (1930) reached a conclusion about the relationships of myriapods that apparently was based on careful morphological studies of many arthropods. He wrote:

> A consideration of the mouth-parts of all four sub-classes of Myriapoda gives the same two results as the consideration of their walking legs, viz., that each of the four sub-classes is more related to the one of the three others than to any order of the Insecta, and that each of the sub-classes is less related to any order of Apterygota than types of the Apterygota are related to the Malacostraca. . . . both mouth-parts and legs in Myriapoda show alterations and reductions which are far from indicating primitive stages, and the entire class is a natural group sharply limited from all Insecta, and less allied to Crustacea than is the case with the Machilidae.

Like Hansen, Snodgrass (1938) did not consider the location of the genital openings as the chief criterion on which to establish the relationships of myriapod classes. He believed that the structure of the legs and the mouth parts and the absence or

presence of fused somites were more important characters than location of genital openings upon which to base a theory of the relationships of the myriapods. His explanation of the origin of heterogoneate conditions of modern arthropods follows:

> . . . a segmental difference in the position of the genital openings is to be explained only as the result of mutations that have been effective in the zone of teloblastic growth, which determines which particular pair of coelomic sacs shall be utilized as genital exits. . . . In the Chilopod . . . there still exists a variability as to the segment of genital ducts, for, though the genital outlet is always on the subterminal segment in Chilopoda . . . the genital segment is not morphologically the same somite in all cases, since the number of somites preceding it may be quite different . . . even among individuals of the same species.

Snodgrass postulated a theory of the phylogenetic relationships of arthropods that is diagrammed in Figure 3.

ANNOTATED KEY TO THE MYRIAPODS OF NORTH CAROLINA

Sixty-eight of the myriapods included in this key were listed in *Insects of North Carolina* (Brimley 1938). Most of the remaining 96 species were collected by the author during 1939 and 1940. Doubtless several species occur in the state which have not yet been discovered and are therefore not included in this key, but it probably covers the myriapods in the Duke Forest very well. Minute species are probably present which will be found only with the use of Berlese or Silvestri funnels.

The identification of many of the diplopods and chilopods was confirmed by Dr. R. V. Chamberlin. Dr. A. E. Michelbacher identified the symphylans. Names of collectors are in parentheses.

The author followed Attems (1930) in designating the larger taxonomic divisions; Chamberlin (1911b, 1912, 1912b, 1912e, 1913, 1917, 1917a, 1925b, 1939) in the arrangement of the Geophilomorpha, Lithobiomorpha, and Fontariidae; and Williams and Hefner (1928) in many of the specific descriptions. In general, natural characteristics were used in making distinctions between groups, but in some instances, for the sake of simplicity, artificial features were used.

1 (2) Antennae with three terminal branches; animals minute.

Class Pauropoda Lubbock 1866.

Many species of this class have been reported from North America, but none have been collected in North Carolina. Undoubtedly, careful searching under stones, bark, and logs and in humus will result in these myriapods being found in this state.

The 12 post-cephalic somites are covered by six dorsal plates or tergites in American species. There are nine pairs of legs, each of which terminates in a single claw. The length is usually less than 1.5 mm. Descriptions of genera and species are in "Pauropoda of North America" (Hilton 1930b).

2 (1) Antennae not branched. 3

3 (86) First pair of post-cephalic appendages never modified as "poison claws" or prehensorial feet. 4

4 (9) One pair of legs to a somite; animals minute.

Class Symphyla Ryder 1880.

Members of this class resemble small white centipedes (Chilopoda) as they move about quickly in damp humus and soil. Adult symphylans have 15 or 22 post-cephalic tergites and 12 pairs of legs. Each leg terminates in 2 claws. The length may be from less than 2 mm. to almost 8 mm.

Descriptions of genera and species are in "Symphyla of North America" (Hilton 1931b). At least three genera occur in North Carolina. 5

5 (6) First leg pair reduced to clawless papilla-like processes. Symphylella Silvestri 1902.

Collected in the Duke Forest throughout the year (Causey).

6 (5) First leg pair well developed and over half as long as the following pair. 7

7 (8) Last tergite with a broad pit in the caudal margin; no long sensory bristles on the lateral margins of the tergites. *Scutigerella causeyae* Michelbacher (MS name).

Collected in the Duke Forest throughout the year (Causey).

8 (7) Last tergite without such a pit.

Hanseniella elegans Michelbacher (MS name)

This species is very common in the green houses of Mr. C. R. Hibberd, Durham. Workmen there reported that it does not damage living plant tissues.

9 (4) Most of the post-cephalic somites bear two pairs of legs; animals seldom minute. Class Diplopoda Latreille 1802. 10

10 (11) Thirteen pairs of legs in adult animals. Subclass Pselaphognatha Latzel 1884.

Polyxenus fasciculatus Say 1821

Body 2.5 mm. long; color pale brown; feet white; short bristles on head and body and clumps of longer bristles on sides of each somite; short thick antennae; eleven post-cephalic somites in adult.

Collected in the Duke Forest in July (Cornwell), December, and February (Causey) and at Fort Fisher in April (Wray); found in pine and red gum logs and in the soil in A_0 horizon; not common.

11 (10) Twenty-eight or more pairs of legs in adults animals. Subclass Chilognatha Latreille 1802. 12

12 (17) Mouth parts reduced and suctorial; the ninth and tenth pairs of legs modified as gonopods in the male; eight pairs of walking legs anterior to gonopods. Order Colobognatha Brandt 1834. 13

13 (16) Tergites neither sulcate nor covered with short stiff hairs; lateral carinae not well developed; ocelli present. 14

14 (15) Adult animals with from 30 to 55 post-cephalic somites.

Polyzonium rosalbum (Cope 1870)

Octoglena bivirgata Wood 1864. Proc. Phil. Acad. Sci., p.186.

Polyzonium bivirgatum Cook and Loomis 1928. Proc. Nat. Mus., 72:18.

Color yellowish white to pale rose; length up to 20 mm.; body about six times as long as broad; dorsum convex; 2-4 ocelli on each side of head; legs short, scarcely reaching edge of body; can coil spirally; secretion of repugnatorial glands has a distinctly camphor-like odor.

Collected near Durham and at Huckleberry Springs in October (Causey) and at Silver in November (Johnson).

15 (14) Adult animal with 28 post-cephalic somites.

Buotus carolinus Chamberlin 1940

Color whitish; length of the only specimen, apparently a female not fully grown, 4 mm.; antennae relatively large and distally heavy; median longitudinal sulcus; keels of collum project conspicuously laterad; succeeding tergites conspicuously elevated except adjacent to their anterior and posterior margins, where they are lower; two large setae on anal tergite; three shorter setal in a series on each anal valve.

Collected in a pine-hardwood forest near Durham in December (Causey).

16 (13) Tergites produced into wide lateral carinae; distinct longitudinal and transverse sutures; dorsal tubercles; ocelli absent.

Platydesmus lecontii (Wood 1864)

Dorsum rosy; legs, antennae, and head principally yellow; body depressed; about four times as long as broad; tergites bear two transverse rows of tubercles; numerous short hairs on body; 4-8 setiferous tubercles on last tergite; length 8-21 mm.; 29-55 body somites.

Collected at Balsam Gap and at Sunburst in May (Brimley) and at Soco Falls in April (Causey); found in the soil in the F layer of the A_o horizon; not common.

17 (12) Chewing mouth parts; seven pairs of legs anterior to gonopods; the eighth and ninth, or only the eighth, pairs of walking legs modified as gonopods in the male; gonopods either external or within a pouch in the body. Order Eugnatha Attems 1898. 18

18 (19) Body round or almost round in cross-section; 26 or more post-cephalic somites. 20

19 (18) Body not round in cross-section; dorsum flat or convex; adult animals with from 19 to 22, but usually 20, post-cephalic somites; male with one pair of walking legs less than female; eighth pair of legs of male modified as gonopods; tergites produced into wide or narrow lateral carinae; ocelli absent. Order Polydesmoidea Pocock 1887. 22

20 (21) All sternites posterior to seventh free from pleurites; 26 or more post-cephalic somites in adult animals. Order Nematophora Verhoeff 1913. 64

21 (20) All sternites posterior to seventh fused with pleurites; adult animals with 40 or more post-cephalic somites. Order Juliformia Attems 1930. 70

22 (23) Tergites with deep transverse furrows, smooth; lateral carinae narrow; body narrow; dorsum almost flat. Family Strongylosmidae Cook 1895.

Orthomorpha gracilis (Koch 1847)

Adults with 20 body somites; dorsum chestnut brown to black; legs, sternites, and carinae lighter; larvae cream, gray, or light brown; gonopods as in Figure 45; length 18-22 mm.; width 2.0-2.2 mm.

Collected in greenhouses in Durham throughout the year (Causey); probably widely distributed in greenhouses in North Carolina; collected in a bamboo thicket in Durham in March and April (Causey) and in pine litter in the Duke Forest in April (Causey), in compost holes at Raleigh in August and December, and at Stanford in July (Wray); introduced from the tropics.

23 (22) Tergites without transvers furrows, smooth or granulated; body sometimes very wide; dorsum flat or convex. 24

24 (25) Femora, and sometimes coxa of legs, bears a pointed spine; dorsum convex. Fontariidae Attems 1930.

Members of this family are usually large and brightly colored. Adults have 20 post-cephalic somites; males have 30 pairs of walking legs and females 31 pairs. Genera and species are determined from the structure of the male gonopods. Chamberlin's division of the genus Fontaria into several genera will be followed in this key. 34

25 (24) Femora of legs without a spine. 26

26 (27) Anal tergite triangular.. 28

27 (26) Anal tergite blunt, quadrate. Family Platyrhachidae Pocock 1895.

Euryurus erythropygus (Brandt 1841)

Dorsum dark gray or almost black, red-coral spots on posterior median edge of each tergite and on posterior angles of lateral carinae; feet dull yellow; males with 30 pairs of legs; females with 31; gonopods as in Figure 4; length 30 mm.; width 4-5 mm.; adults with 20 post-cephalic somites.

Collected in the Duke Forest in June, July, February (Cornwell), October, and November; found in logs and in the A_0 horizon of the soil; larvae with 15, 17, 18, and 19 post-cepahlic somites found in October and November (Causey).

Individuals of this species are often found in groups of 10-15 or more within a radius of several inches.

28 (33) Dorsum tuberculate and flat or almost flat. 29

29 (32) Adult animals with 19 body somites; males with 28 pairs of legs, females with 29. Family Sphaerotrichopidae Attems 1914.. 30

30 (31) Repugnatorial pore surrounded by a round swelling; most tergites bear 5 or 6 transverse rows of tubercles; length 12-16 mm.

Scytonotus *granulatus* (Say 1821)

Brown, paler below; each tergite covered with 4-5 rows of setiferous granules; length 12-16 mm.; width 1.5-1.7 mm.; legs of female one-third shorter and one-half as thick as legs of male; gonopods as in Figure 5.

Collected in Raleigh in February and November (Brimley), at Linville in October, and in the Duke Forest in October, November, and December (Causey); found in decaying logs and in the soil in the A_0 horizon in pine-hardwood stands; never very numerous; probably generally distributed over the state.

31 (30) Repugnatorial pore surrounded by a long oval swelling; most tergites bear 3 transverse rows of tubercles; length 7-12.5 mm.

Brachydesmus *dux* Chamberlin (MS name)

Brown, paler below; posterior margin of most tergites toothed; resembles *Scytonotus* *granulatus* and *Polydesmus* *serratus* but can be distinguished with certainty by the difference in the shape of the male gonopods (Fig. 6).

Collected at Durham in and near a bamboo thicket on the Woman's College campus in February, March, and April (Causey).

32 (29) Adult animals with 20 body somites; males with 30 pairs of legs, females with 31. Polydesmidae Attems 1914.

Polydesmus serratus Say 1821

Brown or reddish brown; tergites with two rows of elevations or knots, 4 in a row; on either side outside these elevations the surface is convex; posterior margin of tergites with several denticulations; gonopods as in Figure 7; size extremely variable; length 17-35 mm.; width 3-6 mm.

Collected at Raleigh in July and December (Brimley), at Lake Waccamaw in September (Causey), during every month of the year in the Duke Forest (Pearse, Cornwell, Causey), at Silva in November (Johnson), Soco Falls in April, at Linville in October (Causey), and on Mt. Pisgah in July and August (Wray); found breeding at Raleigh in May and November (Brimley), in the Duke Forest in October and November (Causey), at Soco Falls in April, and at Linville in November (Causey); seldom present in large numbers; often found in somewhat dry pine or pine-hardwood woods.

33 (28) Dorsum smooth and convex; body wide; lateral carinae large, smooth, not serrate. Leptodesmidae Attems 1898.

Leptodesmus hispidipes (Wood 1864)

Dorsum dark, olive brown, sometimes with yellowish spots and a mid-dorsal black line; carinae short and with edges thickened; feet rough with closely set stiff hairs; antennae dark, scarcely clavate, and coarsely pubescent; last tergite triangular and with long hairs; length 28 mm.; gonopods of the male short and thick, with a curved, hairy terminal spine, as in Figure 8.

Collected in the Duke Forest (Cornwell).

34 (35) Principal blade of gonopods long and coiled 48

35 (34) Principal blade of gonopods relatively short and curved, but not coiled. 36

36 (37) Principal blade of gonopods short, stout, and deeply forked at distal end as shown in Figure 9.

Zinaria virginensis (Drury 1770)

Fontaria virginensis Bollman 1893. Bull. U. S. Nat. Mus. 46:123.

Dorsum dilute chestnut; venter, legs, lateral carinae, and a narrow band on caudal margins of tergites dull pink; collum banded anteriorly with pink; sterna have caudal margins produced at sides into blunt tubercles; coxae unarmed; length 30-35 mm.; width 7 mm.

Collected at Raleigh and at Southern Pines (Brimley).

37 (36) Principal blade of gonopods not deeply forked at end.. 38

38 (42) Principal blade of gonopods thick, subcylindrical, narrows abruptly into a slender, acutely tipped chitinous blade which curves mesad to reach the tip of the blade on the opposite gonopod; this blade bears about 3 ordinary setae proximally and just beyond this a thicker bacilliform seta; distal portion of blade glabrous. Nannaria Chamberlin 1918. 39

39 (40) Caudal branch of gonopod almost reaches end of main branch; it makes a decided double or sigmoid flexure, the acute tip bending across that of the other one, a short acute spur at the level of the first flexure on the ventral side.

Nannaria minor Chamberlin 1918

Dorsum smoky brown; carinae yellowish; dark median longitudinal dorsal line in posterior portion; antennae and legs yellowish; coxae unarmed; length of male 27 mm.; width 5.5 mm.

Collected at Raleigh in February and December (Brimley). Since this species occurs in East Tennessee (Chamberlin 1918) it probably will be found in the adjoining section of North Carolina. *Nannaria media* Chamberlin 1918 also occurs in East Tennessee.

40 (41) Principal processes of gonopods gradually narrowing distad, glabrous distal region short and curving abruptly mesad; anterior process slender and extending obliquely mesodistad.

Nannaria infesta Chamberlin 1918

Carinae and caudal borders of tergites red; elsewhere olive and olive gray; vertigial sulcus very deep, extending below on a level with centers of antennal sockets; sternites without processes; length of male 35 mm.; width 5.5 mm.

Collected at Cranberry in August (Thaxter).

41 (40) The acuminate process of the subcylindrical division of the gonopods projects dorsocephalad and is much shorter than in *N. minor* and thus far shorter than the principal blade.

Nannaria conservata Chamberlin (MS name)

Processes on carinae of nineteenth tergite extend directly caudal, their ends convexly rounded; processes of other carinae becoming more angular in going forward; sternal processes at bases of legs following the seventh are short and conical; processes of coxae of second legs cylindrical and rather stout; length of male 19 mm.

Collected in the Duke Forest in November (Causey).

42 (45) Principal blade of gonopods extends ventrad in line with axis of proximal joint and is but slightly curved, not coiled, and bears below middle on mesal side a single spine or process; proximal joint glabrous or nearly so, bearing from mesal side at distal end a

single uncinate process, the apex of which lies in a pit or furrow on the mesal side of the main blade. Aporiaria Chamberlin 1928. 43

43 (44) Gonopods as in Figure 26.

Aporiaria carolina Chamberlin 1939

Head and antennae black or nearly black; dorsum solid black except for a yellow spot at each end of the collum and on the posterior portion of the ordinary keels; under surface of keels, and sides of body, and anal valves black; venter yellow; legs yellow except third articles which are black and the fourth which are dusky; processes of coxae of second legs cylindrical; coxae of other legs and sternites without processes; length, male 32 mm.; female 36 mm.; width 5.2 and 7.0 mm.

Collected in April at Soco Falls, near Waynesville (Causey).

44 (43) Gonopods as in Figure 27.

Aporiaria geniculata Chamberlin 1939

Head dark above, elsewhere yellow; antennae yellow proximally, darker distally; dorsum black or nearly black; keels yellow; narrow yellow band across caudal margin of tergites; venter and legs yellow; coxae and sternites without processes except the conical ones of the second sternite; length 27 mm.; width 5 mm.

Collected in April at Soco Falls, near Waynesville (Causey).

45 (42) Principal blade of gonopods extends cephalad, a little curved toward or beyond middle of length and expanded into a small laminate plate at distal end; a short, typically laminate spur toward its base. Mimuloria Chamberlin 1928. 46

46 (47) Gonopods as in Figure 25.

Mimuloria ducilla Chamberlin 1939

Dorsum, head, and antennae black; labral borders of head yellow; collum with caudolateral corners and a transversely elongate median spot on anterior border yellow; ordinary tergites trimaculate; caudolateral corners of keels and a transverse median spot bordering caudal margin yellow; venter brownish yellow; legs light yellow; sternal processes of second body somite of male acutely conical, no processes on other sternites or on the coxae.

Collected in April at Soco Falls, near Waynesville (Causey).

47 (46) Gonopods of the Mimuloria type but otherwise than those figured.

Mimuloria pelior Chamberlin (MS name)

Colected in the Duke Forest (Pearse).

Mimuloria furficer Chamberlin (MS name)

Collected in the Pisgah Forest in June (Pearse).

48 (55, 56) Principal blade of gonopods coiled in corkscrew twist; small spur at its base. Apheloria Chamberlin 1921. 49

49 (50) Gonopods as in Figure 10.

Apheloria coriacea (Koch 1847)

Fontaria coriacea Koch 1847. Syst. Myr., p.141.

Dorsum blackish chestnut; lateral carinae and posterior border of tergites margined with a yellow, verging to pink, band of varying width; legs and venter lemon yellow; coxae and femorae spined; length 38-51 mm.; width 9-11 mm.

Collected in the Duke Forest (Pearse, Cornwell, Causey).

50 (51) Gonopods as in Figure 11.

Apheloria aspila Chamberlin 1939

Head mostly black, but in part brown like the antennae; dorsum black with ectocaudal half of keels

yellow; sides, venter, and legs yellow; length 41 mm.; width 10 mm.

Collected at Soco Falls in April (Causey) in the A_0 horizon of the soil in deciduous forests.

51 (52) Gonopods as in Figure 12.

Apheloria tigana Chamberlin 1939

Dorsum black; caudal lateral portions of keels in the preserved specimens brown, the light color extending in a lateral stripe forward along lateral border; head black above and brown below; sides, venter, and legs light brown or yellow; form of basal spur especially distinct; length 40 mm.; width 10 mm.

Collected at Raleigh (Brimley) and in the Duke Forest (Causey).

52 (53) Gonopods as in Figure 13.

Apheloria unake Chamberlin 1939

Dorsum, head, and antennae black; tergites trimaculate, the lateral yellow spots large, occupying caudal part of keels, the median spot small; collum with large lateral spots and on median line with a large anterior spot and either no spot posteriorly or this represented by a vague, small dot; venter and legs yellow; length of male and female holotypes 39 and 45 mm. respectively; width 10 and 11 mm.

Collected in August at Hot Springs (Chamberlin).

53 (54) Gonopods as in Figure 14.

Apheloria waccamana Chamberlin (MS name)

Dorsum dark brown; lateral carinae and a median spot on posterior 6-8 tergites yellow; venter and legs yellow; antennae brown; length of male 37 mm.; width 9-10 mm.

Collected in the Duke Forest throughout the year (Pearse, Cornwell, Causey).

54 (53) Gonopods of the Apheloria type but otherwise than those figured.

Apheloria scholastica Chamberlin (MS name)

Collected in the Duke Forest (Pearse).

Aphelorla brachygon Chamberlin (MS name)

Collected in the Pisgah Forest (Pearse).

Aphelorla acrophor Chamberlin (MS name).

Collected in the Duke Forest (Pearse).

55 (56) Subapical portion of the main blade of the gonopods broadly expanded as shown in Figure 15.

Sigiria scorpio Chamberlin 1939

Head and dorsum dark brown; collum completely surrounded by a red border; red border on posterior margin of tergites and on lateral and posterior edges of carinae; legs red; antennae dark brown; collum with light anterior and posterior border connecting the lateral light areas; antennae brown; length 36-38 mm.; width 8.5-9 mm.

Collected in August between Hot Springs and Paint Rock (Chamberlin) and in April at Soco Falls (Causey).

56 (46) Main blade coiled sigmoidally. Sigmoria Chamberlin 1939.

Members of this genus are large and robust, and the principal blades of the gonopods are characterized by having the blade sigmoidally curved. Of the 6 species included in this key, 4 have been collected in North Carolina and 2 in Tennessee and South Carolina very near North Carolina. Fontaria evides Bollman 1893, now included in this genus, may also occur in North Carolina. 57

57 (58) Gonopods as in Figures 16 and 17.

Sigmoria munda Chamberlin 1939

Dorsum in preserved specimens dark brown to black; carinae yellow; usually a narrow caudal border on tergites also lighter in color; venter and legs light in color as usual; length of male 44 mm.; width 10.5 mm.

Collected in August at Hot Springs and Asheville (Chamberlin).

58 (59) Gonopods as in Figure 18.

Sigmoria aberrans Chamberlin 1939

Dorsum black; carinae orange yellow; antennae brown; venter and legs in preserved specimens yellow; length 39-44 mm.; width 10-11 mm.

Collected in August at Linville Falls (Chamberlin).

60 (61) Gonopods as in Figures 19 and 20.

Sigmoria conclusa Chamberlin 1939

Dorsum black; carinae yellow-orange; antennae dark brown; legs yellow; length of male 40 mm.; width 10.2 mm.

Collected in August at Altapass, Tennessee (Chamberlin).

61 (62) Gonopods as in Figures 21 and 22.

Sigmoria divergens Chamberlin 1939

Dorsum black; caudal margins of tergites and lateral margins of carinae red; on the sides a red line runs from carinae to bases of legs; legs with first two joints yellow, others pinkish red; caudal and anterior borders of collum red; antennae brown; in preserved specimens the red color usually fades out; length 40 mm.; width 10 mm.

Collected in August at Landrum, South Carolina (Chamberlin).

62 (61) Gonopods as in Figures 23 and 24.

Sigmoria mariona Chamberlin 1939

Dorsum black; carinae and caudal borders of tergites yellow; borders of collum yellow; antennae brown; legs and venter yellow; length 40 mm.; width 10-11 mm.

Collected in August at Marion (Chamberlin).

63 (62) Distal fourth of principal blade of gonopods much expanded; basal spine stout, bifid; two lateral lobes, the first trifid, the other bifid.

Sigmoria rubromarginata (Bollman 1887)

Dorsum dark brown; anterior border of collum and posterior borders of all tergites red; legs and venter yellow; length of male, 38 mm.; width 10 mm.

Collected at Balsam (Atkinson).

64 (65) Dorsum rough with deep furrows that result in numerous longitudinal keels. 66

65 (64) Dorsum smooth except for six setigerous tubercles on each body somite. 68

66 (67) Adults with about 61 post-cephalic somites; length 35-55 mm.; locomotion very rapid.

Callipus lactarius Risso 1826

Callipus lactarius Risso 1826. Hist. nat. d. Europe mer., 5:150.

Spirostrephon lactarius Brandt 1840. Recueil, 90.

Lysiopetalum lactarium Packard 1883. Am. Nat. 17:555.

Usually dark brown to almost black; about 17 keels on each somite; preanal scale broadly triangular; about 115 pairs of legs; length 35-55 mm.; width 2-3 mm.

Collected in the Duke Forest throughout the year (Pearse, Cornwell, Causey) in logs or A_0 and A_1 horizons of the soil; at Linville in October (Causey); at Silva in November (Johnson); Raleigh (Brimley); numerous.

This millipede is characterized by its very rapid movement and the peculiar odor of the white secretion from the repugnatorial glands.

67 (66) Adults with 30 body somites; length 12-13 mm.

Striaria causeyae Chamberlin 1940

Gray-brown; posterior half of tergites bear prominent longitudinal keels, usually 13 on each somite; last tergite deeply three-lobed.

Four specimens were collected in the Duke Forest in December (Causey).

68 (69) White or cream; adults about 4 mm. long; width 0.5 mm.; 28 body somites.

Tynopus dux Chamberlin 1940

Eyes crescent-shape, consist of 6 ocelli; setigerous tubercles prominent; setae long.

Only 2 specimens were collected, one in Mr. C. R. Hibberd's greenhouse, Durham, in October, and the other in the Duke Forest in December (Causey).

69 (68) Light brown; about 15 mm. long; 30 body somites.

Cleidogona caesioannulata (Wood 1865)

Broad gray annulus and gray spots on each tergite; thin longitudinal mid-dorsal line extends the length of the body; antennae slender, extend to fifth tergite; setae pointed, spine-like; length 14-16 mm.; width 1.5-1.7 mm.

Collected in the Duke Forest in June, July, September, October, November (Pearse, Cornwell, Causey) and at Raleigh in October (Brimley); never very abundant but usually appears in every collection; probably well distributed over the state.

70 (71) Gonopods concealed. 72

71 (70) Gonopods partly or entirely exposed.. 76

72 (73) First five post-cephalic somites bear four pairs of legs.

Spirobolus marginatus (Say 1821)

Dark brown; a dark red band on the posterior margin of each somite; tergites finely punctuate; eyes subtriangular and consist of 30-40 ocelli; antennae short, curved, lying close to head; first two post-cephalic somites not closed ventrally; first tergite with anterior border nearly straight and its sides obliquely truncate; second tergite has its sides much produced and bent forward so as to embrace the first tergite; anal scale triangular; somites 47-57; pairs of legs 86-106; length 40-116 mm.; width 5-10 mm.

Collected in the Duke Forest during the entire year (Pearse, Cornwell, Causey), at Lake Waccamaw in September, at Bent Creek Camp, near Asheville, in April (Causey) and June (Pearse); found in the A_0 and A_1 horizons of the soil and in logs; eggs found in June (Pearse); larval stages found throughout the year (Causey).

73 (72) First four post-cephalic somites bear three pairs of legs. 74

74 (75) Dorsum yellow, with a median black line.

Brachyiulus pusillus (Leach 1814)

Repugnatorial pores black; eyes triangular and composed of about 40 ocelli; length 12 mm.; width 0.9 mm.

Collected at Durham in and near a bamboo thicket on the Woman's College campus in February, March, and April (Causey).

75 (74) Dorsum brown.

Diploiulus luscus (Meinert 1868)

Dorsum dark to pale brown; eyes triangular, composed of 17-25 ocelli; exoskeleton shining in females, dull in males; length 11-16 mm.; males shorter; pairs of feet, 61-73.

Collected in greenhouses in Durham throughout the year.

This species is reported to be a serious pest in some greenhouses, but the writer found no greenhouse workers who believe that it does any damage.

76 (79) Ocelli few, 4-10 in a linear series. 77

77 (78) Ocelli 4-6, length up to 56 mm.

Cambala annulata (Say 1821)

Dorsum light rosy brown; venter, feet, and antennae light; exoskeleton deeply sulcate longitudinally, resulting in 16 elevated ridges on each tergite, except the first and last; collum large; gonopods half concealed to nearly concealed.

Collected in the Duke Forest throughout the year (Pearse, Cornwell, Causey), at Waynesville and near Asheville in April (Causey), at Balsam, and at Chapel Hill (Atkinson); found in the A_0 and A_1 horizons of the soil; relatively common.

78 (77) Ocelli 8-9; length 9-14 mm.

Nopoiulus minutus Menge 1851

Brown, a lateral row of ovate black spots; antennae black and white and as long as body width; three white spots and a dark band form a triangle between the eyes; repugnatorial pore in the posterior division of each somite not touching the transverse suture; last somite rounded, pilose; anal scale small, rounded, pilose; 38-42 somites; 55-77 pairs of legs; 0.5-0.8 mm. in width; introduced from Europe.

Collected in the Duke Forest (Causey); most common under loose bark of logs.

79 (80) Ocelli many, 40-80, in a triangular or subtrapezoidal arrangement; second pair of legs greatly stunted in both sexes; first pair of legs much enlarged; gonopods exposed; gonopods replace both pairs of legs on the seventh post-cephalic somite. Parajulus Humbert and Saussure 1869.

This genus has recently been split into a several genera (Chamberlin 1840) on the basis of the structure of the gonopods. 80

80 (81) Anal spine sharply decurved into a pronounced hook.

Parajulus canadensis (Newport 1844).

Dorsum dark brown, almost black; sides with a series of yellow, conglomerate spots; length 25 mm.; width 1.6 mm.

One female collected in pine litter in the Duke Forest in September (Causey).

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

81 (80) Anal spine lacking or reduced; if present, it extends scarcely or not at all beyond the anal valves. 82

82 (83) Anal valves and posterior somite sparsely or not at all pilose; gonopods as in Figure 29.

Parajulus impressus (Say 1821)

Dorsum chestnut brown; median line black; lateral rows of black spots; indistinct rows of large dark spots near base of legs; lateral blotches paler; feet pale; all somites striate; 51-53 post-cephalic somites; 93-97 pairs of legs; length 28-35 mm.; width 1.8-2.2 mm.

Collected at Raleigh in March (Brimley).

83 (82) Anal valves and posterior somite densely pilose. . . . 84

84 (85) Repugnatorial pores partly hidden by transverse suture, which is sharply emarginate; gonopods as in Figure 30.

Parajulus pennsylvanicus (Brandt 1841)

Dark brown to purplish black; feet paler; striate beneath and at caudal margin of each plate; antennae dark with all joints white tipped; body slender, rough, and densely pilose; most somites with two rows of setae; enlarged first legs of male very broad, pilose and marked posteriorly with median black line; anal scale small, rounded; 55-65 somites; 101-123 pairs of feet; length 38-52 mm.; width 1.8-2.5 mm.

Collected throughout the year in the Duke Forest (Pearse, Cornwell, Causey); at Soco Gap Falls in April (Causey); and at Realigh in February, March, May, and December (Brimley); relatively common.

85 (84) Repugnatorial pore not touching transverse suture, which is straight; gonopods otherwise.

Parajulus ectenes Bollman 1887

Very dark brown, almost black, light spots more or less confluent and indistinct; joints of antennae tipped with white; legs brown; somites pilose and sulcate; anal scale obtuse, angular; 67 somites; length 46-54 mm.; 120-118 pairs of feet; width 1.6-1.8 mm.

Collected at Chapel Hill (Atkinson), which is the type locality.

86 (3) First pair of post-cephalic appendages modified into "poison-claws," known also as malapedes, maxillipedes, or prehensorial appendages. Class Chilopoda Latreille 1802. 87

87 (88) 21 or more pairs of legs; young hatch with adult number of legs; neither sex with gonopods. Subclass Epimorpha Haase 1880. 89

88 (87) 15 pairs of legs in adults; young hatch with 7 pairs of legs; gonopods larger in female than in male (Fig. 37). Subclass Anamorpha Haase 1880. 122

89 (111) 29 or more pairs of legs. Order Geophilomorpha Pocock 1895. 90

90 (98) Median piece of labrum large and armed with fringe of teeth or spines; lateral pieces of labrum small, free edges smooth and unarmed (Fig. 31); head small as in Figure 33. Subfamily Linoteniinae Chamberlin 1912. 91

91 (94) Claws of prehensors unarmed, conspicuously excavated at proximal end dorsally, constricted (Fig. 33b). Agothothus Bollman 1893. 92

92 (93) Head and prehensors as in Figures 33a and 33b.

Agothothus *gracilis* (Harger 1872)

Yellow; head and prosternum brownish; prehensorial claws long, when closed nearly reach front margin of head, sparsely hirsute; ultimate article of antennae longer than preceding 2; anal legs longer than penult legs; pairs of legs in male 77, in female 81.

This widely distributed species has been collected at Johnson City, Tennessee, so it probably occurs in North Carolina.

93 (92) Otherwise.

Agothothus carolinus Chamberlin (MS name)

Collected in the Duke Forest (Pearse, Cornwell).

94 (91) Claws of prehensors armed within with a single large tooth, not excavated proximately (Fig. 34). Linotenia Koch 1847. 95

95 (96) Pairs of legs of male 47-55, female 48-59.

Linotenia fulva (Sager 1856)

Yellow-orange; cephalic plate subtriangular, crossed by a faint frontal suture; broad basal plate overlaps caudal angle of cephalic plate; last ventral plate very narrow; numerous coxopleural pores; length 25-33 mm.

Collected at Saluda (Chamberlin) and in the Duke Forest (Pearse, Cornwell, Causey).

96 (97) Pairs of legs 37-45.

Linotenia bidens (Wood 1863)

Red-orange; polished; cephalic plate punctuate; prehensorial claw with a rather small basal tooth; coxae of anal legs large with 20 or more irregularly arranged small pits; anal legs of male thick; length 40-50 mm.

Collected in the Duke Forest (Pearse, Cornwell, Causey) and at Raleigh (Brimley).

98 (90) Median piece of labrum relatively very small; lateral pieces large; free edge armed with few to many spinescent processes (Fig. 32); head longer than wide. 99

99 (100) Second maxillae with a very strongly chitinized oblique, pleurosternal suture; anal legs have six

articles beyond the coxapleurae and are armed with claws. Subfamily Chilenophilinae Chamberlin 1912.

Gnathomerium umbricatium (McNeill 1887)

Head deep orange; body light orange; malapedes pilose, with longer hairs mesad, deeply punctate, each with four teeth, the two outer longer than the two inner; legs and tergites densely pilose; 49 pairs of legs; caudal pair of legs slender, scarcely modified; length 21 mm.

Collected at several places in western North Carolina (Chamberlin, Causey) and in the Duke Forest (Pearse, Causey).

100 (99) Second maxillae without any such chitinous suture. Subfamily Geophilinae Chamberlin 1912. 101

101 (106) Prehensorial feet mostly not extending beyond anterior margin of head, the joints unarmed within or only obscurely so; last ventral plate mostly wide to very wide. Geophilus Leach 1814. 102

102 (105) Frontal plate discrete. 103

103 (104) Coxopleurae of last leg-bearing somite with from 5 to many small pores.

Geophilus mordax Meinert 1885

Geophilus virginensis Bollman 1899. Proc. U. S. Nat Mus., p.346.

Geophilus atopleurus Chamberlin 1909. Ann. Ent. Soc. Amer. 2:181.

Usually red, but sometimes pinkish or yellowish brown; color fades quicky in alcohol; slender; narrowed posteriorly; prehensorial feet scarcely reaching front of head; cephalic lamina suboval, covering anterior angles of basal plate which is four times as wide as long; prebasal lamina shows; tergites bisulcate; last ventral plate wide; coxae of anal legs not strongly inflated; number of coxopleural pores variable; 49-51 pairs of legs; length 35 mm.

Collected at Raleigh (Brimley), Marian, Salisbury, Hot Springs (Chamberlin), and in the Duke Forest (Pearse, Cornwell, Causey).

104 (103) Coxae of last leg-bearing somite with two large pits, which are covered by the last ventral plate.

Geophilus rubens Say 1821

Testaceous; head and prehensorial feet darker; sometimes a black, interrupted band along the dorsum; prehensorial claws extend beyond front of head; prebasal plate exposed; last ventral plate very wide; pairs of legs of male 49-50, female 51-53.

Collected in the Duke Forest (Pearse, Causey); occurs under bark of pine trees frequently.

105 (102) Frontal plate not discrete.

Geophilus varians McNeill 1887

Body yellow, deeper and brighter toward head, which is orange; anterior and posterior margins of cephalic plate straight and equal, lateral margins evenly curved; antennae pilose; prehensorial feet each with one small tooth; caudal legs slightly swollen; pairs of legs 51-55; length 19 mm.

Collected at Raleigh (Brimley) and in the Duke Forest (Pearse, Cornwell, Causey).

106 (101) Prehensorial feet much exposed from above, extending well beyond anterior margin of head, the joints distinctly denticulate within; last ventral plate either wide or narrow. 107

107 (110) Last ventral plate very wide; coxopleural pores aggregated and opening into two large pits on each side adjacent to and covered by edge of last ventral plate; anal legs clawless, composed of seven articles beyond coxapleura. Arenophilus Chamberlin 1912. . . 108

108 (109) Ventral pores in a transverse area extending across each sternal plate, or nearly so, in front of caudal edge.

Arenophilus bipuncticeps (Wood 1862)

Light orange; head deep orange; prehensorial appendage armed with four indistinct teeth; pairs of legs, male 61-67, female 63-69; length 48 mm.

Collected in Durham at Doyle greenhouse (Causey).

109 (108) Ventral pores in a median circular area on each sternal plate.

Arenophilus watsingus Chamberlin 1912

Yellow; head light reddish brown; prehensorial claw with a small subcylindrical blunt tooth at base; first joint of prehensorial appendage with a very low, obtuse denticule; other joints and prosternum unarmed (Fig. 36); pairs of legs, male 33-59, female 53-63; length of male type 27 mm.

Collected in the Duke Forest (Pearse), Lake Waccamaw (Causey), Hot Springs and Brown's Summit (Chamberlin).

110 (107) Last ventral plate narrow; pores of coxopleura not aggregated and opening into pits; anal legs with six joints beyond coxopleura, and with claws; legs 41-47 pairs.

Pachymerium ferrugineum (C. L. Koch 1835)

Orange, dark spotted, an interrupted fuscous band on the posterior two-thirds of the dorsum; cephalic plate punctuate; malapedes pilose, two-toothed, the anterior one black, the posterior one orange and less conspicuous; last sternite small; coxopleurum large and with small round pores; anal pores present; first pair of feet as large as the second; pairs of legs in male 41-45, in female 43-47; length of male 20-25 mm., female 30-35 mm.

Collected in the Duke Forest (Pearse, Cornwell, Causey).

111 (89) Pairs of legs 21 or 23. Order Scolopendromorpha Pocock 1895. 112

112 (119) Pairs of legs 21. 113

113 (116) Eyes present, composed of 4 ocelli; tarsi of all legs triarticulate. 114

114 (115) Second tarsal joint of all legs unarmed; anal legs armed with 9-12 spines; antennae composed of 17 articles, pubescent, swollen at base.

Scolopendra woodii Meinert 1886

Body yellow-brown, more or less varied with green; head and antennae blue-green; distal tip or two-thirds of legs blue-green; remaining part of legs creamy white or light tan; first tergite with a transverse suture near anterior margin; length 46-60 mm.; width 3.7-4.5 mm.

Collected at Raleigh, Beaufort, Southern Pines (Brimley) and in the Duke Forest (Pearse, Gray Cornwell, Causey); females found in logs with 12 eggs July 12, 1939, and with 17 white larvae, July 31, 1939; often found in A_0 and A_1 horizons in the soil.

115 (114) Second tarsal joint, except on anal legs, armed; anal legs moderately short and stout, with 10-18 spines; antennae composed of 23 articles, generally not pubescent.

Scolopendra viridis Say 1822

Greenish brown; feet pale; cephalic tergite broadly ovate, sparsely punctuate; anal legs subcylindrical, rather robust, armed with 10-19 spines; first body somite smallest, the third the next smallest; tergites frequently bordered posteriorly with dark green or sometimes yellowish green; posterior feet occasionally tipped with blue; sometimes a dark longitudinal mid-dorsal stripe; length 51-70 mm.

Collected in the Duke Forest (Pearse, Cornwell).

116 (113) Eyes absent; tarsi, except those of penultimate and anal legs, biarticulate. 117

117 (118) Anal legs very thick and short, tips cross, basal part without spines.

Theatops posticus (Say 1821)

Orange; finely punctuate; head polished; feet lighter in color; last tergite very large, quadrate, larger than preceding tergite; length 36-50 mm.; width 3.5-4 mm.

Collected at Raleigh, Greensboro, Hendersonville (Brimley), Mt. Pisgah in July (Wray), and the Duke Forest throughout the year (Pearse, Cornwell, Causey); found under bark of logs and in A_0 and A_1 horizons in the soil.

118 (117) Anal legs bear many short spines and are twice as thick and almost twice as long as any other legs, almost parallel.

Cryptops hyalinus Say 1821

Pale orange-yellow; smooth; flat; two longitudinal lines; head and antennae ferrugineous; length 12-17 mm.; width 0.9-1.1 mm.

Very common in the Duke Forest under bark of logs and in A_0 and A_1 horizons of the soil; collected in April at Soco Falls (Causey) and at Raleigh (Brimley); probably well distributed over the state; eggs found in May in the Duke Forest.

119 (112) Pairs of legs 23. 120

120 (121) Tarsi of anal legs densely hirsute; dorsum olive brown; head, first, and last somites reddish brown.

Scolopocryptops nigridus McNeill 1887

Antennae brown and sparsely hirsute; caudal legs with first tarsal joint sparsely and second and third tarsal joints densely pilose; median anterior margin of prehensorial plate slightly convex and with a thin black margin; no teeth on coxae; length 26-40 mm.

Collected at Raleigh, Chapel Hill (Brimley), and in the Duke Forest (Causey); not common; occurs chiefly in the A_0 horizon of the soil and in logs.

121 (120) Tarsi of anal legs not densely hirsute; bright yellow or reddish orange.

Otocryptops sexspinosus (Say 1821)

Last tergite broad, but narrowed behind; anal legs long, smooth, femora with one or two conspicuous spines mesad; antennae yellow, hirsute; median anterior margin of prehensorial plate nearly straight; small tooth at base of prehensorial coxae; length to 75 mm.

Collected at Raleigh, Chapel Hill, Southern Pines, Salem (Brimley), Silva (Johnson), Linville (Causey), Mt. Pisgah (Wrey), and in the Duke Forest throughout the year; found in the A_0 and A_1 horizons of the soil and in logs.

This is the largest and one of the most common centipedes in the state. It bites readily with the "poison-claws," and the poison secretion causes a painful irritation that may last two days.

122 (171) Tracheae open through paired spiracles located in the pleural region of a variable number of post-cephalic somites; antennae and legs moderate or short; eyes simple or absent. Order Lithobiomorpha Pocock 1895. 123

123 (124) A single ocellus or none; posterior angles of no dorsal plates produced; a tibial spur usually on all legs; no true articular leg spines; anal pores present. Family Henicopidae Pocock 1901.

Lamyctes pius Chamberlin 1912

Dorsum brown, legs yellowish; antennae composed of 28 or 29 articles; each eye consists of a single ocellus; prosternal teeth 3 - 3, the outer one reduced; coxal pores 2, 3, 3, 3; body covered sparsely with short hairs; length 7.5-9.5 mm.

Collected at Hot Springs and Asheville (Chamberlin).

124 (123) Ocelli either absent or in a group of several to many on each side; legs bear articular spines; no anal pores in adults. Superfamily Lithobioidea 1917.

> "The spines borne upon the legs of the members of this family are important in the diagnosis of species. It is customary to enumerate those occurring on the ventral aspect of the first, penult and ultimate pairs, those found at the distal ends of the joints from trochanter to tibia inclusive being listed in order; thus, 1, 3, 3, 1, where trochanter bears one, prefemur 3, femur 3, and tibia 1 [Fig. 38]. The number and arrangement of the ocelli is also of importance in the discrimination of species. It is advantageous to give the number of horizontal series in which the ocelli fall and to enumerate the number of ocelli in these series in order from above ventrad. There is commonly a large single ocellus a little caudad of the main group which is separately reckoned; e.g. 1 and 5, 5, 3, 2. The number of prosternal teeth on the two halves of the prosternum is indicated by the appropriate figures separated by a dash; e.g., 3-3, where the number of teeth on each side is three.
>
> In making use of the keys in the present paper care must be taken to make sure that specimens are fully adult." Chamberlin 1910a, pp.368-369. 125

125 (126) Coxal pores in several series. Family Ethopolidae Chamberlin 1915.

Bothropolys multidentatus (Newport 1845)

Lithobius multidentatus Williams and Hefner 1928. Ohio Biol. Sur. 32:143.

Color varies from light yellowish brown to deep red; antennae composed of 19-24 articles; ocelli 25-40 in 7-8 series; prosternal teeth 7-7 to 9-9; coxal pores numerous, small, round, in 3-5 series; posterior angles of 6, 7, 9, 11, and 13 dorsal plates produced; length 15-27 mm.

Collected at Chapel Hill (Atkinson), Raleigh (Brimley), Catawba (Chamberlin), Linville (Causey), and in the Duke Forest throughout the year (Pearse, Cornwell, Causey).

126 (125) Coxal pores in a single series. 127

127 (128) Claw of female gonopods entire, long, and strongly curved. Family Gosibiidae Chamberlin 1915.

Arenobius manegitus (Chamberlin 1911)

Dorsum brown; antennae short, composed of 20-23 articles; ocelli 10-15 in 3-4 series; prosternal spines very stout, greatly exceeding teeth in size; posterior angles of 9, 11, and 13 dorsal plates produced; anal and penult legs of males thickened and furrowed longitudinally; length 15-17 mm.

Collected at Hot Springs, Catawba, Saluda, and Linville (Chamberlin).

128 (127) Claw of female gonopods bi- or tri-partite. Family Lithobiidae Chamberlin 1915. 129

129 (142) Antennae composed of 20 articles; prosternal teeth 2-2. 130

130 (135) Median incision of prosternum V-shaped; posterior angles of none of dorsal plates produced; coxae pores 2, 3, 3, 2, to 3, 4, 4, 3, small, circular; a small crest of sensory setae at distal end of tibia of anal legs of male; occurs chiefly under bark of logs. Garibius Chamberlin 1913. 131

131 (132) Ocelli 6-8, in 4-5 series.

Garibius branneri (Bollman 1888)

Light brown; prosternal teeth 2-2, small; coxal pores 2, 3, 3, 2 to 3, 4, 4, 3; spines of female gonopods slender, subequal, outer toothed; length 5-10 mm.

Collected at Catawba, Brown's Summit, Asheville (Chamberlin).

132 (131) Ocelli about 14 in 3 series; coxal pores 3, 4, 4, 3, small. 133

133 (134) Dorsal spines of anal and penult legs 1, 0, 2, 1, 0.

Garibius catawbae Chamberlin 1913

Dorsum light brown, legs and venter pale, tarsi darker; spines of twelfth legs $\frac{0,\ 0,\ 2,\ 1,\ 1}{0,\ 0,\ 2,\ 3,\ 2}$; length 8 mm.

Collected at Catawba (Chamberlin).

134 (133) Dorsal spines of anal legs 1, 0, 2, 0, 0; of penult legs 1, 0, 2, 1, 0.

Garibius monticolens Chamberlin 1913

Dorsum light brown; head somewhat orange, legs pale, tarsi darker; spines of twelfth legs $\frac{1,\ 0,\ 2,\ 1,\ 1}{0,\ 0,\ 3,\ 3,\ 2}$; length 8 mm.

Collected at Asheville and Brown's Summit (Chamberlin).

135 (130) Median incision of prosternum semicircular; posterior angles of 11 and 13, or at least 13, dorsal plates more or less produced; coxal pores 2, 2, 2, 2 to 2, 3, 3, 3, very small, circular; a small but conspicuous lobe on distal end of tibia of penult legs of male. Nampabius Chamberlin 1913. 136

136 (137) Third joint of twelfth legs unarmed dorsally; dorsal spines of twelfth legs 0, 0, 0, (1), 1.

Nampabius parienus Chamberlin 1913

Dorsum yellow-orange; antennae orange; legs pale to bright orange; eyes composed of 5 or 6 ocelli in 2 series; spines of anal legs $\frac{0,\ 0,\ 2,\ 0,\ 0}{0,\ 1,\ 1,\ 1,\ 0}$, 2 claws; of the penult $\frac{0,\ 0,\ 2,\ 0,\ 0}{0,\ 1,\ 1,\ 1,\ 0 \text{ or } 0,\ 1,\ 2,\ 1,\ 0}$, 2 claws; of the thirteenth $\frac{0,\ 0,\ 2,\ 0,\ 0}{0,\ 0,\ 0,\ 1,\ 1}$; length 6.5 mm.

Collected at Hot Springs (Chamberlin).

137 (138) Third joint of twelfth legs armed dorsally with one or two spines. 138

138 (140) Dorsal spines of twelfth legs 0, 0, 2, 1, 2.

Nampabius virginiensis Chamberlin 1913

Dorsum dark red-brown; legs pale yellow to orange; eyes composed of 6 or 7 ocelli in 2 series; spines of anal and penult legs $\frac{0,\ 0,\ 2,\ 0,\ 0}{0,\ 1,\ 1,\ 1,\ 0}$; of the thirteenth $\frac{0,\ 0,\ 2,\ 1,\ 0}{0,\ 0,\ 2,\ 1,\ 1}$; length 5 mm.

Collected in the Duke Forest under pine bark (Pearse).

139 (140) Dorsal spines of twelfth legs 0, 0, 1, 1, 2 or 0, 0, 2, 1, 1.

Nampabius carolinensis Chamberlin 1913

Dorsum yellowish; head reddish orange; eyes composed of about 6 ocelli arranged in 2 series; spines of anal legs $\frac{0,\ 0,\ 2,\ 0,\ 0}{0,\ 1,\ 1,\ 1,\ 0}$, 2 claws; of penult $\frac{0,\ 0,\ 2,\ 0,\ 0}{0,\ 1,\ 2,\ 0,\ 1}$, claws; of thirteenth $\frac{0,\ 0,\ 2,\ 1,\ 0}{0,\ 0,\ 2,\ 1,\ 1}$; length 6.5 mm.

Collected in December in a compost hole on Duke University campus (Causey).

140 (141) Dorsal spines of twelfth and thirteenth legs 0, 0, 2, 1, 0; of the eleventh 0, 0, 0, 0, 1.

Nampabius longiceps Chamberlin 1913

Dorsum brown; head reddish; legs and venter pale; eyes composed of 7 or 8 ocelli in 2 series; coxal pores 2, 3, 3, 3, very small; spines of anal and penult legs $\frac{0,\ 0,\ 2,\ 0,\ 0}{0,\ 1,\ 1,\ 1,\ 0}$, 2 claws; of the thirteenth $\frac{0,\ 0,\ 2,\ 1,\ 0}{0,\ 0,\ 1,\ 1,\ 1}$; length 6.5 mm.

Collected at Asheville (Chamberlin).

141 (140) Other species of Nampabius than those described.

Nampabius mycophor Chamberlin (MS name)

Collected in the Duke Forest in September (Causey).

Nampabius waccamawus Chamberlin (MS name).

Collected at Lake Waccamaw in September (Causey).

142 (129) Antennae composed of 19 articles.

Nampabius lundii (Meinert 1886)

Brown; ocelli consist of 6 or 7 ocelli in 3 series; coxal pores 2, 3, 3, 2; length 6.5 mm.

Collected at Asheville and Hot Springs (Chamberlin). The position of this centipede is somewhat doubtful.

143 (129, 142) 21 or more antennal articles. 142

144 (163) One or more segments in the 15 or in the 14 and 15 leg furrowed. 145

145 (158) Posterior angles of no dorsal plates produced conspicuously. 146

146 (147) No ocelli; but a darker spot at the place where they normally are.

Typhlobius coecus (Bollman 1888)

Orange; head and last somites dark; sparsely pilose; head longer than wide; antennae consist of 28 short joints; coxal pores 2, 3, 4, 3, or 3, 3, 3, 3, round; claw of female gonopod long, bipartite, spines slender, inner shorter; length 8.5-11 mm.

Collected at Saluda (Chamberlin).

147 (146) Ocelli present. .148

148 (153) Prosternal teeth 2-2, or occasionally up to 4-4. . .149

149 (152) 9-14 ocelli, usually arranged in 3 series; antennae consist of 25-35 articles; spines of anal legs

$\frac{0,\ 0,\ 2,\ 0,\ 0}{0,\ 1,\ 3,\ 1,\ 0,\ \text{or}\ 0,\ 1,\ 3,\ 2,\ 0}$; of the penult

$\frac{0,\ 0,\ 3,\ 1,\ \text{or}\ 0,\ 0,\ 3,\ 1,\ 1}{0,\ 1,\ 3,\ 3,\ \text{or}\ 0,\ 1,\ 2,\ 3,\ 1}$. Tidabius Chamberlin 1913. 150

150 (151) Ventral spines of anal legs 0, 1, 3, 2, 0.

Tidabius suitus (Chamberlin 1911)

Lithobius cantabrigensis var. *suitus* Chamberlin 1911. Ann. Ent. Soc. Amer. 4:41.

Dorsum brown; antennae purplish to yellowish brown; legs and venter pale; antennae composed of 29 to 32 articles; coxal pores 2, 3, 3, 2 to 3, 4, 4, 3; eyes composed of 8-11 ocelli in 2 or 3 series; spines of thirteenth legs $\frac{0,\ 0,\ 3,\ 1,\ 1}{0,\ 1,\ 3,\ 3,\ 1}$; of the penult $\frac{0,\ 0,\ 3,\ 1,\ 0\ \text{or}\ 0,\ 0,\ 2,\ 1,\ 0}{0,\ 1,\ 3,\ 3,\ 1}$, claws 2; of the anal $\frac{0,\ 0,\ 2,\ 0,\ 0}{0,\ 1,\ 3,\ 2,\ 0}$, 2 claws; length 7-9 mm.

Collected at Hot Springs (Chamberlin).

151 (150) Ventral spines of anal legs 0, 1, 3, 1, 0.

Tidabius tivius Chamberlin 1913

Dorsum violaceous or grey brown; legs and venter pale; antennae composed of 25 to 31 articles; coxal pores 2, 3, 4, 3 to 3, 4, 4, 3; eyes composed of 10 or 11 ocelli in 3 series; spines of the thirteenth legs $\frac{0,\ 0,\ 3,\ 1,\ 1}{0,\ 1,\ 2,\ 3,\ 1\ \text{or}\ 0,\ 1,\ 3,\ 3,\ 1}$; of the penult $\frac{0,\ 0,\ 3,\ 1,\ 0}{0,\ 1,\ 3,\ 3,\ 1}$; of the anal $\frac{0,\ 0,\ 2,\ 0,\ 0}{0,\ 1,\ 3,\ 1,\ 0}$, 2 claws.

Collected in the Duke Forest (Pearse).

152 (149) Ocelli 6 to 9, in 2 or 3 series, antennae usually consist of 24 articles; spines of anal legs $\frac{1,\ 0,\ 3,\ 1,\ 0}{0,\ 1,\ 3,\ 2,\ 0}$; of penult legs $\frac{1,\ 0,\ 3,\ 1,\ 1}{0,\ 1,\ 3,\ 2,\ 1,\ \text{or}\ 0,\ 1,\ 3,\ 2,\ 0}$.

Pampibius paitus (Chamberlin 1911)

Dorsum pale brown; head darker; caudal legs bright yellow; prosternal teeth 2-2; coxal pores 2, 4, 4, 3 to 1, 3, 3, 2, small; in anal legs of

male the fourth joint is strongly swollen and provided at proximal end with a lobe on dorso-mesal surface from the posterior surface of which springs a dense brush of hairs which projects beyond the caudal end of the joint; length 6.5-7 mm.

Collected at Catawba (Chamberlin).

153 (156) Prosternal teeth 5-5 or more. 154

154 (155) Dorsal spines of second legs 0, 0, 3, 2, 1; ventral spines of first legs in adults usually 0, 0, 2, 3, 2; claw of female gonopods entire.

Sozibius providens (Bollman 1887)

Light brown to yellowish; head darker; posterior legs yellow; antennae consist of 28 to 35 articles; ocelli 9 to 15 in 4 or 3 series; prosternal teeth 5-5 to 7-7; coxal pores 3, 4, 4, 3 to 5, 6, 6, 4; length 11 to 14 mm.

Collected in the Duke Forest (Pearse, Cornwell, Causey).

155 (154) Dorsal spines of second pair of legs 0, 0, 2, 2, 1; ventral spines of first legs 0, 0, 2, 2, 1; claw of female gonopods either bipartite or tripartite. . . 156

156 (157) Last pair of coxae alone laterally armed; first five or six pairs with third joint bearing but 2 dorsal spines.

Sozibius pennsylvanicus Chamberlin 1922

Light to dark brown; head and first dorsal plate darker; posterior legs bright yellow; antennae 27 or 28 articles; 9 to 15 ocelli in 3 or 4 series; prosternal teeth mostly 5-5; coxal pores 2, 3, 3, 2 to 3, 4, 4, 4; length 8 to 10 mm.

Collected in the Duke Forest (Causey).

157 (156) Last 2 pairs of coxae laterally armed; only the first 3 or 4 pairs of legs with but 2 dorsal spines on third joint.

Sozibius *tuobukus* (Chamberlin 1911)

Light brown to yellow; posterior somites darker; posterior legs yellow; antennae consist of 25 to 30 articles; 9 to 18 ocelli in 4 or 3 series; prosternal teeth 5-5 or 6-6; coxal pores 3, 4, 4, 3 to 5, 6, 6, 5; length 9 to 13 mm.

Collected at Brown's Summit, Linville Falls (Chamberlin), and in the Duke Forest (Causey) in December.

156 (145) Posterior angles of 9, 11, 13, and sometimes 6, 7, 9 dorsal plates with produced.

Paitobius Chamberlin 1912.

Prosternal teeth 2-2, of which the inner one on each side is always borne conspicuously farther forward than the outer, the line tangent to apices of teeth curving cephalad from sides to middle; spine at ectad angle bristle-like; anterior margin narrow.

Paitobius *dux* Chamberlin (MS name)

Collected in Mr. C. N. Hibberd's greenhouse, Durham (Causey).

Paitobius *diversus* Chamberlin (MS name)

Collected from a pine log in October in the Duke Forest (Causey).

Paitobius *eutypus* Chamberlin (MS name)

Collected at Linville in October (Causey). . . 157

157 (160) Posterior angles of 6, 7, 9, 11 and 13 dorsal plates produced; ventral spines of anal legs 1, 3, 2, 1; of penult 1, 3, 3, 2.

Paitobius *arienus* (Chamberlin 1911)

Brown; anal legs purplish brown; antennae consist of 32 to 34 articles; ocelli 14 to 20 in 4 or 5 series; coxal pores 3, 4, 4, 3 to 4, 5, 5, 4; length 10.5 to 11.5 mm.

Collected at Hot Springs in August (Chamberlin).

160 (161) Posterior angles of 7, 9, 11, and 13 dorsal plates produced; ventral spines of anal legs 1, 3, 2, 0; of penult 1, 3, 2, 1.

Paitobius caroline (Chamberlin 1911)

Yellowish to dark brown; antennae usually consist of 30 to 35 articles; 11 to 16 ocelli in 3 or 4 series; coxal pores 3, 4, 4, 3 to 4, 5, 4, 3; length 7 to 7.5 mm.

Collected at Asheville (Chamberlin).

161 (162) Posterior angles of 9, 11, and 13 dorsal plates produced; ventral spines of anal legs 1, 3, 2, 1; of penult 1, 3, 3, 2.

Paitobius naiwatus (Chamberlin 1911)

Light to dark brown; often purplish; antennae of 32 to 36 articles; ocelli 10 to 16 in 3 or 4 series; coxal pores 3, 4, 4, 3 to 5, 6, 5, 4; length 9-13 mm.

Collected at Saluda (Chamberlin).

162 (161) Posterior angles of 11 and 13 or of none of dorsal plates produced; anal leg with two claws.

Paitobius zinus (Chamberlin 1911)

Brown, violaceous tinge; antennae of 28 to 35 articles; ocelli 11 to 16 in 3 or 4 series; coxal pores 2, 3, 3, 2 or 3, 4, 4, 3; length 7.5 to 10 mm.

Collected at Brown's Summit (Chamberlin).

163 (144) Segments in the fourteenth and fifteenth leg pairs seldom furrowed; if so, only in the male; prosternal teeth more than 2-2. 164

164 (167) Posterior angles of 7, 9, 11, and 13 dorsal plates produced; fourth article of anal legs of male specially thickened and with its dorsal surface or else the

entire article bowed ventrad; prosternal teeth 5-5 to 10-10; coxal pores mostly transverse; length 17-30 mm. Neolithobius Stuxberg 1875. 165

165 (166) Penult legs with but one claw.

Neolithobius mordax (L. Koch 1862)

Dorsum brown, antennae pale; legs and venter testaceous to dark brown; eyes composed of 27 to 50 ocelli in 6 to 8 series; antennae composed of 35 to 39 articles; coxal pores 6, 6, 6, 5 to 11, 11, 11, 9; length 20-30 mm.

Collected in the Duke Forest (Pearse).

166 (165) Penult legs with 3 claws.

Neolithobius latzelii (Meinert 1886)

Dorsum dark brown, antennae brown, legs and venter testaceous; 35-47 ocelli in 7-9 series; antennae composed of 31-34 articles; coxal pores variable, frequently 5, 6, 6, 5, elliptic and circular; length 16-19 mm.

Collected at Brown's Summit (Chamberlin), Chapel Hill (Atkinson), and in the Duke Forest in September (Causey).

167 (164) Posterior angles of only the 9, 11, and 13 dorsal plates produced; anal legs of male not conspicuously modified; prosternal teeth 4-4 to 10-10; coxal pores mostly transverse; length 11.5 to 30 mm. Lithobius Leach 1815. . 168

168 (169) Length 18-30 mm.

Lithobius forficatus (Linne 1756)

Dorsum brownish yellow to chestnut; a median dorsal paler line; antennae and venter brownish yellow to chestnut; eyes composed of 22-40 ocelli in 5-8 series; antennae composed of 36-49 articles, pubescent; prosternal teeth 5-5 to 7-7; coxal pores 6, 6, 6, 5 to 12, 12, 10, 10, large, elliptic to almost circular (Fig. 38).

Collected at Raleigh (Brimley); Asheville, Hot Springs (Chamberlin); the Duke Forest, and Mr. C. N. Hibberd's greenhouses at Durham (Causey).

169 (170) Length 11.5 to 15 mm.

Lithobius atkinsoni Bollman 1887

Dorsum and antennae yellowish brown to chestnut; venter and legs yellow to light orange; eyes composed of 13 to 23 ocelli in 3 or 4 series; antennae composed of 21 to 33 articles; prosternal teeth 4-4 to 7-7; coxal pores 3, 4, 4, 3 to 6, 7, 7, 5, circular or elliptic.

Collected at Balsam (Atkinson).

170 (169) Otherwise.

Lithobius apheles Chamberlin (MS name)

Collected at Linville in October (Causey).

171 (122) Tracheae open through 7 unpaired spiracles arranged along the median dorsal line; antennae and tarsi much elongated; eyes compound. Order Scutigeromorpha Pocock 1895.

Scutigera coleoptrata (Linnaeus 1759)

Scutigera forceps Meinert. Proc. Am. Phil. Soc. (1885):171.

Color variable, olive green to greenish yellow, with median blue, green, or black lines; lateral interrupted lines; length 16-28 mm.; width 3-4 mm.

Occurs in cellars, basements, dark corners of houses, and occasionally under stones, logs, or bark of trees near buildings.

ECOLOGICAL OBSERVATIONS AND EXPERIMENTS

A Quadrat Study of the Distribution of Myriapods in the Duke Forest

The author decided upon the quadrat method for collection of myriapods in the Duke Forest because it, if correctly followed, furnishes a background upon which to work out some of the problems concerned with distribution and density of myriapod populations. There is no record that the quadrat method has ever been used before for myriapods. Writers usually list species and give the localities of collections; some (Verhoeff 1930) have given an idea of the density of population by recording the number of specimens collected within a stated period of time.

1. Methods

Quadrat collections were made in the Duke Forest during October, November, and December, 1939. The precipitation during those months, as reported by the Durham, North Carolina, weather station, was 2.24, 1.41, and 2.06 inches respectively. This represented a total departure of 2.77 inches below the average of the 19 year record.

The principal cover types in the Duke Forest were classified on the basis of the overstory trees as follows: pine, composed

chiefly of Pinus taeda and P. echinata; pine-hardwood, predominantly pines and oaks and red gum; upland hardwood, chiefly several species of oaks; and bottomland hardwood, usually red gum and yellow poplar or river birch and sycamore.

The quadrats measured 1.5 m by 1.5 m. Each one was located at a place that was typical of a particular forest type. The A_0 horizon, or litter layers, and the A_1 horizon of the soil to a depth of 8 cm were carefully examined for the presence of myriapods. Records were kept of the soil layers from which all myriapods were collected.

Records of the following physical conditions were taken at each quadrat: air temperature 0.5 m above the ground, soil temperatures at depths of 3 cm and 8 cm in the A_1 horizon, and hydrogen-ion concentration (with a Hellige soil tester) at a depth of 3 cm in the A_1 horizon. Samples of the A_1 horizon from a depth of 5 to 7 cm were taken to the laboratory in tightly closed tin boxes and dried at a temperature of 95° C two weeks in order to determine the moisture content in percentage of oven-dry weight.

2. Observations

The cover type in which each quadrat was located is given in the following list; the series of numbers represent temperatures in degrees centigrade of (1) the air at a height of 0.5 m from the ground, (2) the A_1 horizon of the soil at a depth of 3 cm and (3) 8 cm, and (4) the moisture percentage of the oven-dry weight of the A_1 horizon at a depth of 5 to 7 cm.

Quadrat 1. Pine-hardwood; litter mainly from hardwood trees; sandy soil; 17.0; 15.0; 14.0.

Quadrat 2. Upland hardwood; soil very rocky; ground well shaded, covered with much moss and few leaves; steep hillside; 16.0; 15.0; 14.0; 44.9.

Quadrat 3. Sycamore-dogwood-tulip poplar flood plain; no F and H layers in the litter; soil fine, very compact; 21.0; 16.0; 14.0.

Quadrat 4. Pine-sycamore stand; soil rocky and hard; 21.0; 17.0; 16.0; 56.6.

Quadrat 5. Pine-hardwood, pine predominated; 9.0; 11.0; 12.5; 18.9.

Quadrat 6. Pine-hardwood, pine predominated; 9.0; 11.0; 12.0; 15.0.

Quadrat 7. Bottomland hardwood; ground covered by drift of hardwood limbs, twigs, and leaves from 12 to 30 cm thick; soil sandy, packed; 8.5; 9.9; 9.7; 38.2.

Quadrat 8. Pine-hardwood; 15 m from Quadrat 7, 4 m higher, and above the level usually flooded; thin litter layer; soil rocky; 8.5; 10.0; 10.1; 57.1.

Quadrat 9. Upland hardwood, mainly scrub oaks; litter layer about 8 cm thick; soil rocky; 11.3; 10.0; 9.0; 18.2.

Quadrat 10. Upland hardwood, mainly elm, oak, and hickory; litter layer about 10 cm thick; clay soil; hilltop; 11.5; 10.2; 9.8; 28.1.

Quadrat 11. Pine-hardwood; litter thin; soil rocky; hilltop; 11.8; 10.0; 9.2; 17.8.

Quadrat 12. Pine-hardwood, pine predominated; gently sloping hillside; loose sandy loam; 9.0; 7.0; 7.0; 17.4.

Quadrat 13. Pine-hardwood; about 95 m from Quadrat 12; mixed litter, but fewer pine needles than in the litter from Quadrat 12; sandy loam; 9.0; 7.4; 7.2; 15.3.

Quadrat 14. Pine stand about twenty years old; litter about 10 cm thick; sandy soil; 11.0; 10.0; 7.5; 6.9.

Quadrat 15. Pine stand 50-60 years old; litter about 12 cm thick; sandy loam; 11.0; 10.0; 7.8; 11.4.

Quadrat 16. Pine-hardwood; litter about 10 cm thick, mainly pine needles and Lonicera japonica; 10.0; 9.0; 8.5; 20.5.

Quadrat 17. Bottomland hardwood; dark sandy loam; 6.5; 6.0; 6.0; 32.4.

Quadrat 18. Cut-over area, formerly oak stand; no litter; loose sandy loam; 11.0; 9.0; 6.3; 23.3.

Quadrat 19. Pine stand about twenty years old; litter contained oak leaves from a nearby oak stand; 11.0; 8.2; 6.2; 11.9.

Quadrat 20. Pine stand about fifteen years old; litter sparse; ground covered mostly with lichens, moss, and a few tall herbs; 1.5; 1.5; 2.0; 17.3.

Quadrat 21. Stand of scrub oaks and thirty years old pines; about 95 m from Quadrat 20; litter about 5 cm deep; 2.0; 3.0; 5.0; 27.6.

Quadrat 22. Open stand of large oaks and mature pines; litter about 5 cm deep; 2.0; 2.9; 5.0; 28.4.

Quadrat 23. Open stand, mainly oak, hickory, and ash; litter thin; south hillside; soil rocky; 3.5; 5.0; 5.0; 30.7.

The moisture percentage of the oven-dry weight of the soil ranged between 6.9 and 57.1. Hydrogen-ion concentration ranged between 5.0 and 6.0. The greatest difference between air and soil temperature was 7.0° C. The extremes in soil temperature at a depth of 3 cm in the A_1 horizon were 17.0° C and 1.5° C.

The numbers and species of myriapods collected from each quadrat are given in Table 1. Two hundred and twenty-eight myriapods were collected from the 23 quadrats; 5 per cent were symphylans, 33 per cent were chilopods, and 57 per cent were diplopods. The numbers collected from individual quadrats ranged between 0, from 2 quadrats, and 48. All of the symphylans, 44 per cent of the chilopods, and 81 per cent of the diplopods were in the A_1 horizon of the soil; the remaining myriapods were in the A_0 horizon.

Chilopods were more evenly distributed than diplopods were. Species of Geophilomorpha were in 52 per cent of the quadrats, and species of Lithobiomorpha were in 35 per cent. Otocryptops sexspinosus was in 40 per cent of the quadrats. There were no chilopods in the litter layers of 49 per cent of the quadrats or in the A_1 horizon of 35 per cent; 26 per cent of the quadrats contained none.

Diplopods were entirely absent from 26 per cent of the quadrats. The litter layers of 57 per cent and the A_1 horizon of 52 per cent of the quadrats contained no diplopods. The most evenly distributed diplopods were the Juloidea, which were represented by at least three species, and present in 30 per cent of the quadrats. The several species of Family Fonariidae, which

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represented 48 per cent of the total number of myriapods collected, were present in only 23 per cent of the quadrats. No other group, either among the diplopods or the chilopods, was so unevenly distributed as that.

There appeared to be a correlation between soil temperature and the density of myriapod population. The distribution of myriapods in relation to the temperature of the soil at a depth of 3 cm is shown graphically in Figure 39. The breaks in two of the curves are due to the large numbers of Fontariidae in quadrats 7, 16, and 17. At all temperatures encountered there were more myriapods in the soil than in the litter. The greatest number of myriapods, 38 per cent, were collected from quadrats in which the soil at a depth of 3 cm was between 12° and 14° C.

There also appeared to be a correlation between soil moisture and the density of the myriapod population. In the quadrats in which the moisture percentage of the oven-dry weight of the soil from a depth of 5 to 7 cm was between 0° and 10° C, the myriapods were almost four times as numerous in the A_0 horizon as in the A_1 horizon; they represented 8 per cent of the total number collected. Fifteen per cent of the total number were from quadrats in which the moisture percentages were between 11 and 20; there were slightly more myriapods in the A_1 than in the A_0 horizon. Thirty-four per cent were collected at percentages between 21 and 30; myriapods were three times more numerous in the A_1 than in the A_0 horizon. At percentages between 31 and 40 they were nine times more numerous in the A_1 than in the A_0 horizon and represented 42 per cent of the total number. Two per cent of

the myriapods were collected from quadrats where the percentages of soil moisture were between 51 and 60. The relation between soil moisture and population density of myriapods is shown graphically in Figure 40.

The average numbers of myriapods collected in pine, upland hardwood, and pine-hardwood stands (Fig. 41) were almost equal, being between 12.5 and 13 per quadrat. The average number per quadrat collected in bottomland hardwood stands was 58. In quadrats from all four cover types, chilopods were more numerous in the A_0 horizon than diplopods were (Fig. 42). In quadrats in bottomland hardwood and pine-hardwood stands diplopods, due to the large numers of Fontariidae in Quadrats 7, 16, and 17, were more numerous in the A_1 horizon than chilopods; in quadrats in pine and upland hardwood stands chilopods were more numerous than diplopods were (Fig. 43).

3. Discussion

The most significant facts that this survey by quadrats brought out are:

(1) Chilopods are more evenly distributed than diplopods. This probably is because chilopods range far in search of prey, while diplopods tend to aggregate at favorable feeding sites.

(2) During the day chilopods are, in general, more numerous in the A_0 horizon of the soil and diplopods are more numerous in the lower A_0 and upper A_1 horizons. There are exceptions to this statement in both groups of animals. Chilopods find their prey

and room in which to pursue it in the upper stratum of soil, and diplopods find the soft humus on which they feed in the lower stratum.

Food is only one of many interacting factors that affect the vertical and horizontal distribution of myriapods. The chief factors are probably: moisture of the substratum, humidity of the soil air, and texture, quality, and temperature of the soil. Calcium content of the litter on the basis of oven-dry weight varies with the type of plant cover that deposits the litter; in turn, calcium content of litter has a profound influence upon the hydrogen-ion concentration of forest soils (Coile 1937) and upon the animals living in them. Diplopods, which by reason of their diet of humus are necessarily in more intimate contact with their substratum than chilopods are, might be expected to vary more with the type of plant cover than chilopods. This survey was not extensive enough to make the data particularly significant on this point.

Cultures of Myriapods in the Duke Forest

The experiment that will be described in this section was undertaken in order to follow certain activities of some common myriapods during the winter months. It consisted, in brief, of putting boxes which contained a known number of marked myriapods in a typical forest area and then opening them at monthly intervals to make observations.

1. Method

A stand of trees behind the Biology Building, Duke University, was chosen as the site for this experiment. It is typical of much of the Duke Forest. The trees consist largely of an overstory of shortleaf pines about 40 years old and a hardwood understory of elm, oak, ash, and dogwood. In October, 1939, the upper soil profile at this site had the following characteristics:

A_0 horizon.	L layer.	Composed of twigs and needles from pine trees and twigs and leaves from hardwood understory trees; 2 to 8 cm thick.
	F layer.	Composed of matted leaves and twigs; 1 to 3 cm thick.
	H layer.	Approximately 0.7 cm thick; black humus.
A_1 horizon.	Composed of dark brown sandy loam; 5 to 8 cm thick.	
A_2 horizon.	Composed of grayish sandy loam; 5 to 8 cm thick.	
B_1 horizon.	Composed of yellowish red clay; depths of B_1, B_2, and C horizons were not determined.	

A preliminary survey of this stand showed that the most common myriapods there were: *Otocryptops* *sexspinosus*, *Theatops posticus*, various species of Lithobiomorpha and Geophilomorpha, and an unidentified species of the Family Fontariidae. Quadrat 16 (Table 1) was located in this stand of trees.

Thirty-three wooden boxes, which measured 11 x 11 x 9 inches on the outside, and were constructed of 9 x $\frac{3}{4}$ inch pine lumber, were used. In each box there were 6 drainage holes one inch in diameter, two in the bottom and 4 in the sides. Wire screen, 256 meshes to the square inch, was tacked over the holes and the tops to prevent myriapods from escaping.

Between October 21 and November 3, 1939, the boxes were buried one-half meter apart, and with the tops even with the surface of the ground. Each box was carefully filled with soil from the hole in which it was placed so that conditions inside the box would be as nearly as possible like those in the soil before it was disturbed. A short length of well-decayed pine log 15 cm long and 5 cm in diameter was included in the A_0 horizon of each box. Myriapods that had been measured as to length and number of somites, were marked by cutting off an antenna or certain legs. They were put on the A_0 horizon before the wire screen was tacked over the top of each box. The myriapods included were one species of Chilopoda, Otocryptops sexspinosus, and six species of Diplopoda: Spirobolus marginatus, Callipus lactarius, Polydesmus serratus, Apheloria coriacea, Fontaria sp., and Orthomorpha gracilis. Only one species was put in each box.

Seven boxes, each of which contained several specimens of one of the species of myriapods listed, were opened at intervals of one month. Records were made of the temperatures of the air and soil and the hydrogen-ion concentration of the A_1 horizon. The soil was carefully searched for myriapods; their positions were noted, and they were taken to the laboratory to determine whether growth and regeneration of appendages had occurred.

2. Observations

The dates and physical conditions when the boxes were opened are given below; the series of numbers represent temperatures

in degrees centigrade (1) of the air 0.5 m above the ground, (2) of the F layer of the A_0 horizon, and (3) of the A_1 horizon at a depth of 7 cm, and (4) hydrogen-ion concentration of the A_1 horizon at a depth of 7 cm: December 21, 1939, 7.8, 7.0, 6.5, 5.8; January 21, 1940, 0.0, 0.5, 3.0, 5.9; February 22, 1940, 6.0, 5.0, 4.0, 5.8; March 21, 1940, 13.0, 10.0, 8.0, 6.0; April 4, 1940, 20.0, 17.8, 15.0, 6.0.

Box 1. Otocryptops sexspinosus. Five specimens ranging in length from 66 to 27 mm; 1 that measured 66 mm recovered Dec. 21; under log; no changes; termites in soil.

Box 2. Otocryptops sexspinosus. Five specimens ranging in length from 60 to 32 mm; 1 that measured 60 mm recovered Jan. 21; under log; no changes; termites in soil.

Box 3. Otocryptops sexspinosus. Five specimens ranging in length from 57 to 36 mm; none recovered Feb. 22; termites, earthworms, thysanurans in soil.

Box 4. Otocryptops sexspinosus. Five specimens ranging in length from 72 to 34 mm; 1 that measured 55 mm recovered Mar. 21; in A_0 horizon; no change except all of the left anal leg was absent, whereas only four segments had been cut off; termites in soil.

Box 5. Otocryptops sexspinosus. Five specimens ranging in length from 64 to 28 mm; 1 that measured 50 mm recovered April 4; 12 cm deep in A_2 horizon; no changes; earthworms in soil.

Box 6. Spirobolus marginatus. Four specimens ranging in length from 102 to 34 mm; all recovered Dec. 21; coiled in A_1 horizon 7 to 9 cm from surface; no changes.

Box 7. *Spirobolus marginatus*. Four specimens ranging in length from 84 to 36 mm; all recovered Jan. 21; coiled in A_1 horizon 4 to 8 cm from the surface; no changes.

Box 8. *Spirobolus marginatus*. Five specimens ranging in length from 100 to 27 mm; all recovered Feb. 22; coiled in A_1 horizon 4 to 7 cm from surface; no changes.

Box 9. *Spirobolus marginatus*. Five specimens ranging in length from 70 to 31 mm; all recovered Mar. 21; coiled in A_1 horizon 2 to 12 cm from surface; no regeneration; 1 was pale as if molted recently, and increased from 31 mm to 35 mm in length, but still with 47 post-cephalic somites.

Box 10. *Spirobolus marginatus*. Five specimens ranging in length from 85 to 31 mm; 4 recovered Mar. 4; coiled in A_1 horizon 1 to 6 cm from surface; 1 increased in length from 82 to 90 mm; no other changes, a burrow 1.5 cm diameter, 11 cm deep, with about 100 excrement pellets at bottom.

Box 11. *Callipus lactarius*. Seven specimens ranging in length from 58 to 24 mm; 2 recovered Dec. 21; moving about in A_0 horizon; no changes noted other than that they were darker than in October.

Box 12. *Callipus lactarius*. Five specimens ranging in length from 53 to 25 mm; 2 recovered Jan. 21; under log; no changes.

Box 13. *Callipus lactarius*. Seven specimens ranging in length from 55 to 26 mm; 4 recovered Feb. 22; inside or under log; no changes.

Box 14. Callipus lactarius. Six specimens ranging in length from 56 to 35 mm; 2 recovered Mar. 21, 1 in A_0 horizon and 1 under log; no changes.

Box 15. Callipus lactarius. Five specimens ranging in length from 57 to 24 mm; 2 recovered April 4; 1 in A_0 horizon and 1 under log; no changes.

Box 16. Polydesmus serratus. Five specimens, 3 with 19 post-cephalic somites and 2 adults; none recovered Dec. 21.

Box 17. Polydesmus serratus. Five specimens, 1 with 19 post-cephalic somites and 4 adults; 3 adults recovered Jan. 21; under log; no changes.

Box 18. Polydesmus serratus. Five specimens, 3 with 19 post-cephalic somites and 2 adults; 1 larva recovered Feb. 22; under log.

Box 19. Polydesmus serratus. Six specimens, 3 with 19 post-cephalic somites and 3 adults; 2 adults recovered Mar. 21; in A_0 horizon 2 to 3 cm from surface; no changes.

Box 20. Polydesmus serratus. Five specimens, 4 with 19 post-cephalic somites and 1 adult; 2 larvae recovered April 4; 1 in F layer of A_0 horizon, 1 in cavity of log; no changes.

(All specimens of Apheloria coriacea used were adult; no changes were noted.)

Box 21. Apheloria coriacea. Three specimens; all recovered Dec. 21; 1 in F layer of A_0 horizon and 2 in A_1 horizon 3 cm from surface.

Box 22. Apheloria coriacea. Three specimens; all recovered Jan. 21; 2 in hibernating chambers near log and 1 in A_1 horizon 1 to 3 cm from surface.

Box 23. Apheloria coriacea. Three specimens; 2 recovered Feb. 22; in A_1 horizon 1 to 3 cm from surface.

Box 24. Apheloria coriacea. Three specimens; all recovered Mar. 4; in A_1 horizon 1 to 3 cm from surface.

(The specimens of Fontaria sp. all belonged to the same species and all had 19 post-cephalic somites; no changes were noted in the specimens recovered.)

Box 25. Fontaria sp. Two specimens; none recovered Dec. 21.

Box 26. Fontaria sp. Two specimens; 1 recovered Jan. 21; under log; darker gray; tips of carinae turned from yellow to orange since October.

Box 27. Fontaria sp. Two specimens; 1 recovered Feb. 22; coiled in A_1 horizon 3 cm deep.

Box 28. Fontaria sp. Two specimens; 1 recovered Mar. 21; coiled in A_1 horizon 2 cm from surface.

Box 29. Orthomorpha gracilis. Two adults and 5 larvae of the sixth stadium; 1 larva recovered Dec. 21; in A_1 horizon 8 cm from surface.

Box 30. Orthomorpha gracilis. Two adults and 5 larvae of the sixth stadium; none recovered Jan. 21.

Box 31. Orthomorpha gracilis. Two adults and 5 larvae of the sixth stadium; 2 larvae recovered Feb. 22; under log; no changes.

Box 32. Orthomorpha gracilis. Three adults and 5 larvae of sixth stadium; 4 larvae recovered in A_0 horizon 4 cm from surface; no changes.

Box 33. Orthomorpha gracilis. Three adults and 5 larvae of the sixth stadium; none recovered April 4.

3. Discussion

The four specimens of *Otocryptops sexspinosus* which survived were in four separate boxes; they were among the largest of 25 specimens put into the boxes at the beginning of this experiment. This suggests that there may be a canabalism of *O. sexspinosus* in nature similar to that which occurs in containers in the laboratory.

The survival of 23 of the 23 specimens of *Spirobolus marginatus* is not surprising, since this species is the largest and has the heaviest exoskeleton of all the diplopods that occur in the Duke Forest. The relatively small number of fecal pellets and the absence of runnways or tunnels suggest that this species was quite inactive between December and March. Although more than half of the diplopods were immature, there was evidence that only two molted, or passed into the next larval stadium. One was recovered from under a small log and 22 were recovered from the A_1 horizon of the soil at depths from 1 to 12 cm. There was no correlation between the depth at which *S. marginatus* occurred and the temperature of the soil.

Polydesmus serratus is one of the least hardy of all the diplopods used in this experiment, so the survival of only 8 of 25 is not surprising. It bleeds freely from small injuries and dies from desiccation in a shorter length of time than most other diplopods do. Specimens in this experiment did not migrate vertically, but remained in the A_o horizon and in crevices of logs, which are their normal summer habitats. *Callipus lactarius* also remained under logs and in the Ao horizon; 12 of 32 were recovered.

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Ten of twelve specimens of *Apheloria coriacea* were recovered; eight were at a depth of from 1 to 3 cm in the A_1 horizon and four were under or near logs in the A_0 horizon. *Fontaria sp.* was similarly distributed; three specimens of eight of this species were recovered.

The loss of all adult specimens of *Orthomorpha gracilis* in the experimental boxes was not surprising, since only larvae have been found outside greenhouses in North Carolina during winter months. Later experiments indicated that freezing temperatures are equally fatal to larvae and adults; and that death of adults normally occurs after three or four months or after breeding. Seven of 25 larvae were recovered; one was in the A_1 horizon at a depth of 8 cm and the others were the A_0 horizon. None had molted. In a heated laboratory, sixth instar larvae during the same length of time passed from the sixth stadium, through the seventh, and into the eighth.

Of the seven species of myriapods under observation, *Spirobolus marginatus*, with its round, smooth body, occurred deepest in the soil. This was the only species in which any change in a larva was observed. It is suggested that *S. marginatus* migrates vertically to escape winter cold. The meager data also indicate that vertical migration of *Callipus lactarius*, *Polydesmus serratus*, *Fontaria sp.*, *Apheloria coriacea*, and larvae of *Orthomorpha gracilis* does not occur or that it is slight. The bodies of these species are either rough or flat and not well suited for tunneling into dense soil.

The Effect of Varied Humidities on Some Myriapods

1. Methods

To test the effect of varied humidities on some myriapods the following procedure was carried out. Desired humidities were obtained by using supersaturated solutions of certain chemical compounds in calcium chloride desiccators. The compounds used and their relative humidity values were: H_2O, 96 per cent; $ZnSO_4$, 88 per cent; KBr, 80 per cent; $NaHSO_4$, 60 per cent; LiCl, 15 per cent; $CaCl_2$(dry), 0 per cent. All of the chemicals were of "C.P." grade; the water was distilled. Tests were made with a dewpoint apparatus to check the humidities obtained during the present experiments. They were found to vary from the theoretical values as Sweetman (1933) indicated. Sufficient liquid was used to cover the bottom of the desiccators; the rims were greased with petroleum jelly to prevent evaporation of the liquid. Air temperatures between 29° and 31° C were maintained throughout the experiment. Myriapods recently brought in from the Duke Forest were put into the desiccators in beakers; at 24-hour intervals they were removed and weighed. After death they were dried 2 days at a temperature of 90° C in order to obtain the dry weight.

2. Results

Spirobolus marginatus lost water more slowly than any other myriapod tested. It lived 16 days in a chamber where the humidity value was 96 per cent, while Cambala annulata lived there 5 days,

Callipus lactarius and *Orthomorpha gracilis* 2 days, and *Polydesmus serratus* 1 day. The rate of desiccation of *Spirobolus marginatus* is shown in Table 2. Larger specimens lost moisture less rapidly than smaller ones. Three which weighed 4.9450, 2.9212, and 0.2901 g at the beginning of the experiment died after 10, 6, and 2 days, respectively, at a humidity of 60 per cent. The percentage of water lost before death was in direct proportion to the original weight. At the last 24-hour period that five specimens, which weighed 7.1032, 4.9450, 3.1068, 2.9212, and 0.2901 g at the beginning of the experiment, were alive, they had lost, respectively, 64, 66, 54, 48, and 34 per cent of their total moisture content.

The rate of desiccation of *Cambala annulata* at several humidity values is given in Table 3. The percentage of water lost before death was in direct proportion to the original weight. At the last 24-hour period that three specimens, which weighed 0.4169, 0.3095, and 0.2114 g at the beginning of the experiment, were alive, they had lost, respectively, 52, 47, and 43 per cent of their total water content.

Callipus lactarius and *Orthomorpha gracilis*, as shown in Tables 4 and 5, lost water at approximately the same rate; death from desiccation occurred after about one-half the time that it did for *Cambala annulata* at the humidities tested.

Polydesmus serratus died before the end of the first 24-hour period at all humidity values tested except 96 per cent; at that humidity death occurred before the end of the second 24-hour period.

The rate of desiccation of the chilopod, *Otocryptops sexspinosus*, was similar to that of the diplopod, *Cambala annulata*.

Another chilopod, Linotenia fulva, lost moisture approximately twice as rapidly as Otocryptops sexspinosus (Tables 7 and 8).

3. Discussion

The rate at which water was lost by the myriapods tested varied with humidity, species, and size of the individual. All died, probably of desiccation, at humidity values between 96 and 0 per cent.

The species tested are restricted to habitats where the humidity value of soil air is above 96 per cent the greater part of the time; their presence in a locality indicates a continuously moist condition in the upper soil horizons.

Myriapods may leave their habitats in the soil at night and on very humid days (Verhoeff 1925). Species which lose water most rapidly commonly occur in logs and the lower layers of the A_0 horizon because the organic matter there ordinarily holds a higher percentage of moisture than mineral soil. The smallest myriapods have an advantage over the larger ones in that they can move into deep, moist crevices that large myriapods are unable to enter. The thicker exoskeletons of larger species, however, resist desiccation more effectively than thin exoskeletons of smaller myriapods.

THE HOTHOUSE MILLIPEDE

As an example of a typical diplopod the writer selected the common hothouse millipede, *Orthomorpha gracilis* (C. L. Koch 1847), for intensive study and laboratory experiments. It will therefore be considered in some detail.

Taxonomic Position

Fontaria gracilis Koch 1847, Sys. Myr., p.142; 1863, Die Myr. 2:51.
Polydesmus coarctatus Saussure 1860, Mem. Mex. Myr. p.39, Fig. 18.
Polydesmus (*Paradesmus*) *coarctatus* Humbert and Saussure 1872.
Paradesmus gracilis Latzel 1884, Myr. Aus. Hun. Mon. 2:182, Fig. 70.
Paradesmus dasys Bollman 1887, Proc. U. S. Nat. Mus. 10:619.
Orthomorpha gracilis Bollman 1893, Bull. U. S. Nat. Mus. 46:197.
Oxidus gracilis Cook 1911, Proc. Nat. Mus. 40:625.

The very wide distribution of the hothouse millipede has resulted in a somewhat complicated synonomy. This species was described first as *Fontaria gracilis* (C. L. Koch 1847) and later as *Polydesmus coarctatus* (Saussure 1860). In 1872 Humbert and Saussure referred it to the subgenus Paradesmus of the genus Polydesmus. After Paradesmus was recognized as an independent genus, the hothouse millipede was called *Paradesmus gracilis* (Tomosvary 1879, Latzel 1884). The next change was made in 1893

when Bollman discovered the preoccupation of the name Paradesmus and proposed Orthomorpha as a substitute. Cook (1911) treated the hothouse millipede as the type of a new genus, for which he proposed the name Oxidus. A few recent authors followed him in the use of Oxidus as a generic name (Williams and Hefner 1928, Loomis 1939), but most writers still refer to the hothouse millipede as Orthomorpha gracilis (Attems 1930, Verhoeff 1928, Chamberlin 1939).

The full classification of the hothouse millipede is as follows:

Phylum Arthropoda Siebold and Stannius 1845
Class Diplopoda Latreille 1802
Subclass Chilognatha Leach 1814
Order Polydesmoidea C. L. Koch 1847
Suborder Strongylosomidea Attems 1914
Family Strongylosomidae Cook 1895
Genus Orthomorpha Bollman 1893
Species gracilis C. L. Koch 1847

Morphological Description

The length of male hothouse millipedes is 18.5 to 19.9 mm and the width is 2.0 to 2.2 mm. The females are 19.4 to 22.2 mm long and 2.0 to 2.5 mm wide.

The colors are: dorsum deep chestnut brown or black, carinae bordered with lemon yellow, sides chestnut brown, sterna and basal joints of legs pallid, distal joints of legs and apex of body light brown, antennae and vertex darker than any other parts of the head.

The antennae are slender, filiform or the terminal joints slightly thicker, and joints two to six are nearly equal in length.

The first post-cephalic somite is wider than the head. Its tergite is transversely oblong, slightly convex, twice as broad as long, and with the anterior and posterior corners rounded. The tergites of somites two and three are narrower and shorter than the tergites immediately anterior and posterior to them. Each of the remaining tergites is marked with a slight median impression and a deep transverse furrow across the middle of the posterior subsegments. The anterior subsegments are covered with a rather regular minute reticulation of raised lines. They are separated from the posterior subsegments by a transverse beaded line. The last tergite ends in a pair of prominent rounded, nonsetiferous tubercles separated by a distinct notch with four setiferous punctations.

The lateral carinae are nearly horizontal, less than one-fourth as wide as the body cavity, and with distinctly raised margins. The anterior corners are rounded, and the posterior corners are nearly right angles on the anterior somites and somewhat pointed on the posterior somites. There is a setiferous tubercule near the anterior corner of each carina. The repugnatorial pores are in the lateral edges of the carinae of the 5, 7, 9, 10, 13, and 15 to 19 somites.

The sterna are smooth, sparsely hirsute, and with a broad central depression. At the base of each leg there is a small spine directed caudally. The legs are sparsely hirsute.

The seminal ducts open on the basal joints of the second pair of legs. The gonopods are modified from the first pair of appendages of the seventh post-cephalic somite. They are

composed of a prominent basal joint and an apical joint with a short cushion-like hirsute base, a stout, slightly curved shaft, and four terminal curved prongs. The first prong is short and projects mesad; the second is longer and it expands into a thin triangular blade; the third, the longest, ends in two diverging plates; the fourth is slender; it enters the base of the third prong and remains enclosed for almost its entire length (Fig. 45).

Geographical Distribution

Most species of millipedes are localized in areas which are often very limited in extent. Some have attained a wide distribution in the tropics, however, and a few, of which Orthomorpha gracilis is an outstanding example, have entered temperate regions by way of the congenial conditions in greenhouses.

The hothouse millipede was first described from a greenhouse in Austria (Koch 1847). Since then it has been reported from many tropical lands and islands, numerous hotbeds, and greenhouses, and a few caves in temperate climates. From its original habitat in the East Indies (Cook 1911), it has spread so far that it is the most common and widely distributed representative of the Class Diplopoda (Attems 1899, Cook 1911). The geographical distribution is roughly shown in Figure 44.

There is one record of Orthomorpha gracilis in Africa, but no definite location of the collecting area was given (Brölemann

1909). It was not listed among the 67 species of diplopods collected by the American Museum of Natural History Congo Expedition, 1909-1918 (Chamberlin 1927), nor did Cook refer to it in any of his numerous papers on African diplopods. Since it occurs on the Maderia, Canary (Attems, 1899), and Sechelles Islands (Brölemann 1909) it perhaps is more abundant on the continent of Africa than present records indicate.

Orthomorpha gracilis occurs widely in European greenhouses (Koch 1847, Weber 1882, Attems 1899) and in the southwestern Mediterranean territory (Verhoeff 1928). There is one indefinite record of it in Asia (Brölemann 1909). It has been reported from St. Thomas Island, New Zealand, Viti Islands (Attems 1930), Borneo, Samoa, Malasia, Olinda (Brölemann 1909), Great Loo Choo (Pocock 1895), and the Antilles (Latzel 1884).

Orthomorpha gracilis appears to be widespread in Mexico (Saussure 1860, Humbert and Saussure 1872) and South America. It was reported from Rio de Janeiro, Santos, São Paulo, Paraná, Cubatao, Guatemala, Belém, Piquete, Santa Rita, and Valparaiso in South America, and from the following islands: Fernendo Noronha, Magarita, Dominacan Republic, and the Bermudas (Brölemann 1909, Attems 1899). It was not one of the 67 species of diplopods collected in Colombia, British Guiana, St. Croix, United States Virgin Islands in 1913 and 1914 (Chamberlin 1923), nor was it listed among 150 species of diplopods from the West Indies (Chamberlin 1918).

In North America Orthomorpha gracilis occurs in greenhouses throughout Maryland (Bollman 1893), Kansas (1913) Western Ontario

(Gibson and Ross 1920), New York (Bailey 1928), Ohio (Miley 1927, Williams and Hefner 1928), Michigan (McDaniel 1931), and North Carolina (Brimley 1938). Further study will probably show that it is distributed generally throughout greenhouses in the United States and Canada. It occurs in the open in southern Ohio (Williams and Hefner 1928), southern California, other warmer parts of this country (Chamberlin 1939, personal letter), and North Carolina. It was present in one cave in Pennsylvania, but in none of the 59 other caves in seven eastern states from which Mr. Kenneth Dearolf collected invertebrates (Loomis 1939).

Methods

The hothouse millipedes which were used in this study were collected from the greenhouses of Mr. C. N. Hibbered on Highway 10, one mile west of Durham, North Carolina.

They were present in numbers as great as 359 to a square foot in heavily manured soil on the tables where biennials were growing. They were less numerous on tables on which flower pots were set in cinders and under objects on the ground. The temperature in the greenhouses is kept above 22°C. Plants are thoroughly watered every day, and water drains from the tables rapidly.

Adults and larger larvae were easily found under flower pots and large lumps of manure and loam during the day. Occasionally they moved about on the surface if the plant growth above them was thick enough to cut off most of the light. Smaller

larvae were found in lumps of loam or manure and larger larvae buried from 2 to 10 cm in the soil or cinders.

The millipedes were brought from the greenhouses to the laboratory in bottles or jars and immediately transferred to finger bowls that contained loam, leaf mold, and manure from the greenhouses. If the substratum was kept moist and contained sufficient humus they lived several months. Too little air and too much water resulted in a fungal growth that was fatal; young larvae were less susceptible to this fungal growth than older larvae and adults were. The millipedes under observation were kept in finger bowls and in 50 cc flat-bottom flasks.

Experiments were carried out under the following temperature conditions: (1) a heated laboratory in which the temperature was usually about 22° C, (2) a warm air chamber in which temperatures varied between 29° and 31° C, (3) an unheated room in which temperatures varied between 12° and 20° C, (4) a refrigerator room in which the temperature was usually about 3.5° C, and (5) boxes buried in the ground in the Duke Forest that were subjected to ordinary outdoor variations in temperature between October and April.

The amount of food that adults and larvae of the seventh stadium ate under the first four temperature conditions listed in the preceding paragraph was determined in the following manner: ten specimens of each stadium were placed in 50 cc flasks that contained only sterilized moist sand, manure, leaf mold, or sterilized loam; the faeces were collected and weighed daily for five days.

The toleration of adults and larvae of the seventh stadium to various conditions of humidity was determined as follows: two specimens of each stadium were put into vials that were suspended in screw-lid jars which contained supersaturated solutions of chemical compounds. The chemicals used had the following theoretical relative humidity values: H_2O, 100; $ZnSO_4$, 90; NaCl, 76; $NaHSO_4$, 51; $CaCl_2$, 32; LiCl, 14; $CaCl_2$(dry), 0 (Sweetman 1933). An hour after the millipedes were put into the tightly closed jars, the jars were heated in a water bath slowly enough for the temperature inside to rise one degree centigrade in five minutes. The temperature at which a millipede first appeared to be dead was recorded; then it was removed to cool, wet filter paper so that it might recover if it was not really dead. The effect of low temperatures was determined by placing the millipedes in a refrigerator for varying lengths of time.

Life History

All Diplopoda are anamorphic, i.e., the larvae pass through a number of molts, during each of which the number of legs and somites is increased until the adult number is reached. Additional legs and somites are added in the embryonic region between the anal somite and the somite that was last formed. Polydesmids, polyxenids, and ascospermorphs pass through seven larval stadia, in each of which the numer of somites and leg pairs is constant. Julids also normally pass through seven larval stadia, but after the first, the number of legs and

somites is not definite for each stadium. In the glomerids development is hemianamorphic, i.e., a series of anamorphic molts is followed by three molts which are unaccompanied by increases in number of legs and somites (Verhoeff 1928).

Only one brief reference (McDaniel 1931) to the life history of Orthomorpha gracilis was found. Various phases of the life histories of the following other polydesmid millipedes have been described: Polydesmus complanatus (Fabre 1855), Polydesmus illyricus (Latzel 1884, Verhoeff 1894), Polydesmus abchasius (Lagnau 1911), and Euryurus erythropygus (Miley 1927). The post-embryonic development of Orthomorpha gracilis is similar to that of other polydesmids, but differences have been found.

1. Breeding Habits

McDaniel (1931) found that the one annual generation of hothouse millipedes in Michigan greenhouses was from eggs that were produced in the spring. In Durham, North Carolina, greenhouses, copulating pairs were found from May through June and from September through April; eggs were collected from September through March. It is probable that eggs were produced during the summer months because larvae were collected in September that must have hatched from summer eggs. During the fall and winter months the millipedes copulated in cultures that were kept in a laboratory where the temperature was around 22° C and in an unheated room where the temperature fluctuated between 12° 20° C.

Before copulation a male hothouse millipede transfers spermatic fluid to his gonopods in the following manner: the thorax is bent ventrally so that the openings of the vasa deferentia, which are on the third body somite, are in contact with the gonopods on the seventh somite. A drop of spermatic fluid is then transferred from the vasa deferentia to the gonopods, where it is held by many short bristles on the basal joint. From the gonopods the spermatic fluid is transferred to the vulvae of the female. Fertilization is internal.

During copulation the position of the male and female is as follows: the ventral surface of the posterior 13 or 14 body somites of the male is parallel and dorsal to the anterior 10 or 11 body somites of the female; the legs of the male on those somites are bent closely around the female; in the region of the eighth, ninth, and tenth somites the body of the male is twisted half around the female so that his gonopods are in contact with her vulvae, which open on the third body somite. The head and thorax of the male are directed anteriorly and bent over the head of the female, which is held by the seven anterior pairs of legs of the female. Light or handling usually causes a pair to separate.

The ratio of males to females collected over a period of several months was approximately three to four. The numbers of adults and larvae of the sixth and seventh stadia of each sex in three collections made in January and February are given in Table 9; the total number was 356 males and 273 females.

In October, 1939, 13 pairs of copulating hothouse millipedes were isolated. Each pair was put in a finger bowl that contained

moist loam and manure from greenhouses. Under such conditions millipedes died within a few days after they were segregated. Eleven of the 13 females died before the males did, from 1 to 12 days after the last observed copulation. The males died from 1 to 19 days after the last observed copulation. Only one clutch of eggs was produced by these millipedes; a female observed copulating October 20 laid eggs which hatched November 1; since the longest incubation period observed for eggs at room temperatures was nine days, it is probable that the eggs were laid October 21. All of the females were examined after their death for the presence of eggs in the oviducts; 11 of the 13 contained a few which were almost as large as mature eggs.

2. Oviposition and Incubation of the Eggs

The females deposit their eggs in clutches in small rough cavities from about 4 to 15 mm below the surface of the soil. In neither the greenhouses nor in laboratory cultures were there found any indications of brooding bells or chambers that many polydesmida construct (Verhoeff 1928), nor did the females remain with the eggs. Eggs were collected in September, October, November, December, January, and March. The variety of post-embryonic stadia that were collected in April and May, and from September through April indicated that oviposition may occur during any month of the year in greenhouses under favorable conditions. This absence of a regular annual breeding season is characteristic of many tropical species of animals.

[illegible]

[illegible]

[illegible]

The eggs are creamy yellow or occasionally brown, sperical or oval, quite smooth, and coated with a glutinous fluid which causes them to adhere in clusters. They are rich in yolk in a semi-fluid state and are surrounded by a slightly tough envelop that consists of a vitelline membrane and a chorion (Korschelt and Heider 1899). The diameter is from 0.35 to 0.40 mm and the length from 0.40 to 0.41 mm.

The eggs were deposited in clutches of approximately 300, 150, 63, 50, 17, and 42. One clutch was found in a greenhouse and the others were found in laboratory cultures of millipedes. None of the eggs that rested on glass in a chamber where the theoretical relative humidity was 100 developed, but those under similar conditions on wet filter paper hatched. Eggs on wet filter paper at a temperature of 3.5° C did not develop. Eggs that were kept in the laboratory on a wet substratum hatched in from 5 to 6, 4 to 6, 6 to 8, and 9 to 10 days after they were collected. All were under approximately the same temperature and humidity conditions. No female millipede was found while ovipositing, so the exact dates when clutches of eggs were laid are unknown. The small size of the eggs and the fact that they are deposited in cavities in the soil instead of in brooding chambers makes them difficult to discover. The writer is fairly certain, however, that the eggs in one clutch hatched in either nine or ten days after oviposition. It is probable that variation in the length of incubation is because some females carry their eggs longer after they have been fertilized than others do. It is also probable that the eggs are very sensitive to certain

environmental conditions that were not observed to vary to a significant degree during the periods of incubation.

3. Post-embryonic Development

The post-embryonic development of larvae reared from eggs and of larvae collected in greenhouses was followed. The larvae were kept in a laboratory where the temperature was usually about 22° C. The substratum in the finger bowls in which they were reared was composed of a moist mixture of loam, leafmold, and manure.

The post-embryonic development of Orthomorpha gracilis, as summarized in Table 10, is characterized by seven molts, during each of which the transition from one stadium to the next occurs. Sexual maturity is reached in the eighth stadium. The larvae of each stadium differ in number of body somites, number of legs, size, and amount of pigment present, but the only larva that differs greatly in appearance from the adults is that of the first stadium.

The first instar larvae lie almost motionless with the posterior post-cephalic somites and the head bent ventrad. There are seven post-cephalic somites; the second, third, and fourth bear one pair of legs each; the fifth bears two pairs of limb buds and the sixth one pair. The head is relatively larger than it is at any other stage. The antennae and the legs are sparsely covered with minute bristles. A few larger bristles are on the head and post-cephalic somites (Fig. 49).

Within 18 to 24 hours after hatching the first instar larvae molt. The number of somites is increased to nine, and the number of legs to six pairs. The second, third, fourth, and sixth somites bear one pair of legs each and the fifth two pairs. The second instar larvae become quite active after the first day and move away from the spot where they emerged from the eggs. The yolk plates, which are visible in the larvae of the first stadium are no longer present, and the larvae begin feeding on tiny bits of organic matter. This stadium lasted from 11 to 18 days (Fig. 50).

After the second molt the larvae have 12 post-cephalic somites and 11 pairs of legs. In this and in all succeeding stadia only the second, third, and fourth somites, and also the seventh somite of males, bear one pair of legs. One pair of legs is added to the sixth somite, and two pairs are added to each the seventh and eighth post-cephalic somites. Fabre (1855), vom Rath (1886), and Latzel (1884) stated that the third instar males of Polydesmus sp. have 10 pairs of legs and that the females have 11 pairs. Miley (1927) reported that 60 of the third instar larvae of Euryurus erythropygus and ten third instar larvae of Orthomorpha gracilis which he examined had 11 pairs of legs. The writer carefully examined 50 larvae of the third stadium of Orthomorpha gracilis and found that all of them had 11 pairs of legs. The same larvae were reared to the fourth stadium, and among them were both males and females which are characterized by having 16 and 17 pairs of legs respectively. The third stadium lasted from 13 to 18 days.

With the third molt the number of post-cephalic somites is increased to 15, and two pairs of legs are added to each of the ninth, tenth, and eleventh post-cephalic somites. The males can be distinguished by the presence of one pair of legs, instead of two as in the female, on the seventh somite; in place of the second pair of legs on the seventh somite of the male there are single joints or rudiments of the gonopods. The fourth stadium lasted from 16 to 30 days.

After the fourth molt the larvae have 17 post-cephalic somites and two additional pairs of legs on each of the twelfth, thirteenth, and fourteenth somites. This stadium lasted from 20 to 38 days.

With the fifth molt the post-cephalic somites are increased to 18 and the legs to 26 in the male and 27 in the female. The four additional pairs of legs appear on the fifteenth and sixteenth somites. The sixth stadium lasted from 28 to 46 days.

After the sixth molt the larvae have 19 post-cephalic somites; the males have 28 pairs of legs and the females have 29 pairs. The two additional pairs of legs are added to the seventeenth somite. The seventh stadium lasted from 42 to more than 60 days.

The adult number of somites and legs is reached at the seventh and last molt, and the rudimentary male gonopods of the larval stages are replaced by complete copulatory appendages. The seventh molt adds one somite and two pairs of legs making a total of 20 somites and 30 pairs of legs in adult males and 31 pairs of legs in adult females. Five millipedes reared from

eggs which were collected in September and October passed through the seven larval stadia in 148, 157, 159, 171, and 177 days respectively. Other larvae from the same clutches of eggs were still in the seventh stadium in April, 189 days or more after they hatched. The sum of the smallest numbers of days during which each of the seven stadia lasted was 132; the sum of the greatest numbers of days was 206 or more. The length of stadia varied for individuals from the same clutch of eggs that were reared in the same dish under apparently similar conditions. The length of stadia was prolonged by subjecting the larvae to a prolonged temperature of 3.5° C or by allowing the substratum in the culture dishes to become somewhat dry.

Newly molted adult individuals are of a uniform light cream color except for the dark mid-dorsal line in the region of the heart. Within three weeks after the last molt the color of the dorsum changes from cream to tannish gray, then to brown and finally to deep chestnut brown or black.

It is not definitely known how long adult hothouse millipedes live under ideal conditions. They can be found at all times of the year in greenhouses, but they are never so numerous there as larvae are. Several adult individuals lived more than two months in a laboratory culture; their color at the beginning of that time indicated that they must have been in the adult stage at least three weeks. Adults in cultures in the Duke Forest died, but larvae under the same conditions lived throughout the winter. No adults could be found in a locality on the Woman's College campus, Duke University, where there were many

larvae of the fifth and sixth and a few of the seventh stadia in February, March, and April. Experiments with both larvae and adults under low temperature conditions were equally fatal to both. These data, although not conclusive, indicate that adult hothouse millipedes live three to five months.

4. Molting

The rigid exoskeleton of diplopods prevents growth of the body and must be shed at the end of each stadium. Along with it go the chitinous intima of the fore gut, hind gut, tracheae, glands, etc. Part of the calcium in the exoskeleton is dissolved and absorbed to be used again in the formation of a new exoskeleton. At the same time new internal organs and structures are formed, and a reconstruction, or possibly a complete histolysis, of some of the old organs takes place (Verhoeff 1928, 1937). During part of this complicated process milipedes are completely helpless and immobile, and many pass through it in molting chambers which they prepare.

Orthomorpha gracilis molts seven times; each time definite numbers of somites, from one to three, and legs, from two to five pairs, are added. The new somites always appear between the anal somite and the somite last formed, and the new legs are added to the somites immediately posterior to the somites already bearing legs.

In describing the molting of Orthomorpha gracilis the author will follow the terminology which Verhoeff (1937) used in describing the molting of Rhinocrinus nattereri, a species of the

suborder Spiroboloidea. Verhoeff stated that there are the following four phases in the molting process: a preparatory period, a rigidation period, an intermediate period during which actual shedding of the exoskeleton occurs, and a recovery period.

During the preparatory period *Orthomorpha gracilis* larvae hollow out cavities in the substratum and "plaster" the walls with particles of soil and organic matter which they ingest and discharge from the anus. A molting chamber is somewhat flattened, roughly round or elliptical, and about the length of the larva that makes it.

After the completion of the molting chamber, a larva enters the period of rigidation. The sternites are pushed far apart so that the integument between them is visible, and the body length is about 15 per cent longer than it is at any other time during that particular stadium. Because of internal pressure the mouth parts protrude, the head bends sharply ventrad, vulvae and gonopods turn laterad, limbs stand out motionless, and the larva lies on one side in a loose spiral. The color of a larva of one of the later stadia changes during this period from amber to cream tinged with pale red. This loss of color is due to the fact that the inner layer of the old exoskeleton is being dissolved (Verhoeff 1928). If a larva is touched during this period there is no muscular response because a histolysis of the muscles that move the exoskeleton is in progress. Near the end of this period a leg bud appears for each additional leg that the millipede will have after molting. It is possible to see the new somites

through the thin, clear exoskeleton that will soon be discarded.

The intermediate period, when the actual shedding of the exoskeleton occurs, is shorter than any other phase of the molting process. Internal pressure splits the exoskeleton horizontally between the collum and the head and longitudinally along the mid-ventral line. This pressure is the result of the swollen body and of greatly increased respiratory and heart movements; it slowly forces the exuvae off the body dorsally and leaves the larva white, moist, and weak, with the body coiled and the legs and antennae turned backward.

In the recovery period that follows, the only activities seen at first are heart beat and respiratory movements. Soon a larva slowly bends its legs and antennae, and within three or four hours after molting it begins to crawl about inside the molting chamber. A larva usually devours the exuvae within three or four days, and several days after molting it eats a passageway out of the molting chamber and emerges, still conspicuously white and somewhat soft.

The first molt differs from all of the others in that it is the shortest one and it does not take place within a molting chamber, but at the place where the almost immobile larva hatched from an egg. About twelve hours after hatching three pairs of leg buds can be seen on each larva, and six to twelve hours later the thin exoskeleton splits just behind the head and the larva of the second stadium slowly emerges.

When the time for the second molt approaches larvae have become active, crawled away into crevices in the soil, and

hollowed out for themselves tiny disk-shaped chamber that just fit their curved bodies.

With each succeeding molt the chambers are larger and more carefully constructed and the molting period is longer. In the greenhouses, molting larvae of the second through the fifth stadia were found in the greatest numbers in chambers one to two centimeters below the surface in lumps of fine loam. Although active larvae fed largely on manure where there was an opportunity, they were rarely found in molting chambers in manure. Molting larvae of the sixth and seventh stadia were observed at depths of from three to eight centimeters in loose soil. In the laboratory, molting was easily observed if the individuals were placed in flasks or finger bowls which contained a layer of soil from one-half to two centimeters in depth. Under such conditions the larvae often constructed their molting chambers on the bottom of the containers and the molting process could be seen through the glass. At no time were molting chambers of the hothouse millipede found on top of the soil where some other polydesmids construct theirs (Verhoeff 1928).

The time required for molting between the fifth and sixth stadia was 10 days; the preparatory period lasted 2 days, the rigidation period 4 days, the intermediate period about 6 hours, and the recovery period 4 days. The molting process between the sixth and seventh stadia lasted 14 days, and between the seventh and eighth stadia it lasted about 20 days; the division into periods was similar to that of the molting process between the fifth and sixth stadia. If the molting chamber was destroyed early in the preparatory period the larva constructed

another. Three molting chambers of a larva of the seventh stadium were destroyed; each time the larva built another chamber; finally, after the preparatory period had been prolonged from the usual 4 days to 10, the larva passed into the rigidation period on the surface of the soil.

There was no difference in the time required for larvae to molt at 29° to 31° C and 12° to 20° C. Larvae in the sand did not construct molting chambers at any temperatures, nor did they in loam and leafmold at a temperature of 3.5° C.

Larvae of the sixth stadium that were kept at a temperature of 3.5° C did not molt. Three out of 30 entered the rigidation stage but did not construct molting chambers. Thirty per cent of 80 larvae of the sixth stadium kept at temperatures between 29° and 31° C molted within 40 days after the beginning of the experiment. Fifty per cent of 60 larvae of the same stadium that were kept at temperatures between 12° and 20° C molted. Thirty-eight per cent of those kept on loam, 10 per cent of those on sand, and 36 per cent of those on leafmold molted. The percentages of sixth instar larvae that molted in leafmold, loam, and sand at 3.5°, 12° to 20° C, and 29° to 31° C are given in Table 11. None of the 25 larvae of this stadium that were in outdoor cultures in the Duke Forest between October and March molted.

Behavior

Hothouse millipedes are negatively phototrophic, but this response is not strongly developed because they come to the

surface of soil to feed in subdued light. In greenhouses they are most active at night. The immotile larvae of the first stadium made no response to light stimuli. Larvae of the second stadium remained on the surface of the soil for two or three days; after that they moved into subdued light in crevices of the soil.

Adults that were placed in a narrow beam of light turned away from it, showing no preference for the right or the left. When the left antenna was removed the millipede turned to the left to get out of the ray of light, and vice versa. When both antennae were removed, the millipede moved either to the right or to the left to get out of the ray of light.

When in motion, hothouse millipedes keep their antennae arched and constantly moving; they touch the substratum in front with the tips of the antennae as if testing it before proceding. When feeding or burrowing, the antennae are turned back laterally. If the antennae are touched lightly, the millipede quickly removes them from the source of the stimulus and turns in the opposite direction.

Touching the dorsum and the legs with a needle did not produce the "spiral reflex," but it usually caused the millipede to move if resting or to change the direction of its course if moving. The spiral reflex was usually caused by rough handling.

When turned over on the dorsal surface the millipede began wriggling and moving the legs in an effort to right itself. The head and anterior end turned over first and posterior parts slowly followed.

Hothouse millipedes in small containers with other millipedes, chilopods, spiders, insects, and isopods never showed any fear or agressiveness. In the greenhouses several to many millipedes were often found collected within a small radius; such aggregation indicated the presence of a favorable feeding site rather than a gregarious instinct.

Food Habits

McDaniel (1931) reported that Orthomorpha gracilis is a serious problem in forcing houses because it eats tender shoots and roots of plants. Specimens were received from Sanford, North Carolina, where they were reported to be injurious to trees. Workers in three greenhouses in Durham, North Carolina said that they did not believe that the hothouse millipede injures living plants.

In laboratory experiments Orthomorpha gracilis ate no living plant tissues. Larvae of the sixth stadium and adults at laboratory temperatures did not eat fresh lettuce or sprouting beans; their loss of weight during 12 days when those two plants were offered as food was as great as that lost by control millipedes under similar conditions but without fresh lettuce or sprouting beans.

The amounts of loam, leafmold, and manure that larvae of the seventh stadium and adults ate when subjected to two ranges of temperature are given in Table 12.

All of the millipedes used in this experiment were taken from the same stock culture in the laboratory. When allowed to

feed on manure, leafmold, and loam 24 hours at temperatures from 29° to 31° C, faeces from 10 larvae were 92.4 per cent of the body weight; from 10 adults faeces were 47.4 per cent of the body weight. At temperatures from 12° to 20° C faeces from 10 larvae were 52.8 per cent of the body weight; from 10 adults faeces were 36.1 per cent of the body weight. The mean percentages of the weight of faeces from 20 larvae and adults fed on manure was 60.7; on leafmold, 65.4; and on loam, 45.5. No faeces were produced by either larvae or adults at a temperature of 3.5° C. None ate the fruiting bodies of basidiomycetes or moist, decayed wood at laboratory temperatures. They sometimes ate wet filter paper when loam, manure, or leafmold was available.

Toleration to Variations in Humidity, High and Low Temperatures, and Submersion in Water

At heated laboratory temperatures hothouse millipedes died within 15 hours after they were put into jars in which the relative humidity values were 0 and 14 per cent; at humidity values of 32 and 65 per cent they died within 20 hours; at humidity values of 51 and 76 per cent they died within 23 hours; at 90 per cent they died within 30 hours; and at 100 per cent they lived until death resulted from starvation. Death occurred when the water lost was between 40 and 45 per cent of the total water content of the body.

When the millipedes were subjected to increased temperatures under relative humidity values between 0 and 100 per cent they

died at a temperature between 39° and 39.5° C. There was no apparent correlation between the lethal temperature and relative humidity.

Of 30 larvae of the sixth instar that were subjected to a temperature of 3.5° C, 13 were alive after four months. At this temperature they remained motionless, but if taken into a warm room they began moving and eating within 15 minutes. When these larvae and larvae of the same stadium from cultures in a heated laboratory were subjected to low temperatures just long enough to freeze them quickly, they all recovered; if frozen 30 minutes or longer, larvae from neither group survived. Adult millipedes reacted similarly to freezing temperatures.

Orthomorpha gracilis adults lived from five to seven days when submerged in water. There was considerable wriggling during the first 10 to 12 hours; following that there was little movement except when they were taken out of the water. The body increased 20 per cent in length after five days in water and appeared to be water soaked.

DISCUSSION

Factors which Affect the Distribution of Myriapods

In comparison with the specialized differences of habitat requirements found among members of many other classes of animals, the classes of myriapods may be said to have almost complete ecological unity. With but few exceptions, myriapods pass their lives buried in moist humus layers of the soil or among decaying vegetable matter that serves as food for diplopods and symphylans and furnishes small animals which serve as prey for chilopods and a few diplopods.

The outstanding requirement for the existence of myriapods is a continuous supply of moisture, not necessarily a regular supply, but one that is never completely interrupted. The existence of myriapods in the humus is evidence of moisture continuity of any locality. Since it is impossible for myriapods to extend their range over areas where there is no accumulation of humus that can retain a continuous supply of moisture, they afford unusually valuable evidence regarding earlier extensions of forests or other conditions that would determine their geographical distribution (Cook 1911).

The exoskeleton serves as the first line of defense against desiccation. In chilopods, symphylans, and pauropods it is

largely of chitin; in diplopods it is composed of chitin and various amounts of calcium salts. Species that lack the protection of a well chitinized exoskeleton are more definitely confined to areas where the humus layers in which they live remain moist at all times. Such areas are most commonly found in the tropics, and it is there that myriapods are most abundant and reach their greatest size. Small forms, particularly soil-inhabiting symphylans and geophilids, suffer quickly from desiccation when taken out of their moist habitats. Diplopods in which the exoskeleton is not heavily calcified, as in _Polydesmus_ _serratus_, die from desiccation much sooner than species with heavily calcified exoskeletons, as _Spirobolus_ _marginatus_. Species that suffer from desiccation readily normally occur in logs or in the A_1 horizon of the soil rather than in the A_0 horizon. Savely (1939) suggested that logs are important as hibernacula because of their moisture content rather than the protection they afford at low temperatures. _Spirobolus_ _marginus_ occurs in logs much less frequently than _Polydesmus_ serratus, _Callipus_ _lacturius_, and _Otocryptops_ _sexspinosus_, which are species in which desiccation occurs rapidly.

During periods of drought small myriapods may have an advantage over large types, because minute animals are able to crawl into small cracks and interstices, and thus take advantage of any moisture that exists, even at considerable depths. Larger myriapods in the same locality, although undoubtedly able to endure more exposure to dry air than smaller and more delicate types, are unable to reach small damp cracks. Thus the presence

of large bodied myriapods, such as Spirobolus marginatus, in a locality indicates a continuously moist layer of humus near the surface.

The presence of myriapods in the humus may be limited by the nature of soil (Cook and Loomis 1928). Drying of the surface does not endanger their existence where conditions are such that they can migrate to a moist subsoil. Clays and colloidal soils do not afford sufficient protection, since they crack in drying; myriapods seek lower moist levels in the cracks and are often buried in the soft mud when rains come. If myriapods do exist in regions of colloidal soils, it is because the humus layer is thick enough to hold moisture at all seasons.

Myriapods exist in areas characterized by wide ranges of climatic temperatures. They have been collected from the Arctic Circle to the tropics and from sea level to the tree line of mountains (Verhoeff 1926, Attems 1930). Single species often range widely. Soil and humus temperatures do not often reach the extremes that air temperatures do, so a widely distributed species lives under more nearly uniform temperature conditions than a similarily distributed animal living in the air experiences.

Feeding of adult diplopods and both feeding and development of larvae are inhibited or slowed down by low temperatures. Verhoeff (1926) stated that certain German diplopods completed their life cycle in two years in lowlands, while they required three years at elevations 1500 meters higher. Orthomorpha gracilis larvae survived four months at a temperature of 3.5^{0} C

without feeding or passing into the next larval stadium; at temperatures between 15° and 31° C feeding and development continued. This diplopod passed through the seven larval stadia in a heated laboratory in as few as 148 days; about a year is required at outside temperatures at Durham, North Carolina. It is probable that at localities with shorter summers the length of the larval life might be extended over two or more years. The inability of this species to survive freezing temperatures for more than a few minutes suggests why its northern distribution is limited to heated greenhouses. Other myriapods may react differently to low temperatures. During the winter of 1939-1940 a collection of myriapods was made under a drift of snow 20 cm deep, at a depth of 5 cm in the soil, where the temperature was 2.0° C; symphylans, geophilids, and *Otocryptops sexspinosus* were moving about actively, but *Parajulus sp*. was inactive. Chilopods in experimental cultures were more active at low temperatures than diplopods were under similar conditions. Morgan (1939) stated that diplopods recovered after they were frozen in blocks of ice if they were thawed out slowly. Chilopods occur farther north in Arctic regions than diplopods do (Attems 1930).

High soil temperatures may limit the distribution of myriapods. Cook (1911) reported that a diplopod, *Crabainosoma fonticulorum*, died if held in the hand and exposed to the sunlight a few minutes. Larvae and adults of *Orthomorpha gracilis* died between 39.0° and 39.5° C. Like many soil animals, myriapods are unable to endure temperatures as high as animals that

live in air.

Large diplopods are especially numerous in the mountains of North Carolina; the highest average rainfall and the richest deciduous forests in the state are there. The conditions that result from the combination of these two factors provide a favorable locality for humus-eating myriapods. The sandy costal plain proved to be poor in myriapods; the plant cover, chiefly long-leaf pine and scrub oak, and the sandy soil are not the right combination for the production of a good humus layer. Geophilids were most numerous in collections from that region; these chilopods are small enough to burrow into deep, moist crevices of the soil. At intervals in the costal plain there are remnants of a former luxuriant type of plant cover that was formerly characteristic of that area. Collections from such a site near Lake Waccamaw included large species that also occur in the piedmont region and in the mountains.

Relative humidities of less than 100 per cent are fatal for many humus animals (Davis 1928, Savely 1939). Fidler (1936) showed that the larvae of a scarabid bettle not only require an atmosphere of saturated humidity, but that they must lie on soil that contains more water than would be necessary to maintain a saturated humidity in soil air. Eggs and second instar larvae of Orthomorpha gracilis failed to develop in chambers in which the relative humidity was theoretically 100 per cent, but when they were put on wet filter paper under similar conditions they continued to develop. Eggs of some myriapods have a tougher chorion than those of this species, and may be less susceptible

to desiccation. The larvae of all, however, are subject to desiccation by reason of their small bodies and thin exoskeletons. This problem is overcome in the geophilids by the egg being deposited deeply enough in the soil for the soil air to be saturated. Species that stay nearer the surface, as Spirobolus marginatus, Polydesmus serratus, and Fontaria sp. construct brooding chambers or cocoons from which the larvae do not emerge until after the first two or three larval stadia are passed. Centipedes, especially Scolopendra woodi, move about with the eggs and larvae adhering to their bodies, and presumably carry them to situations where optimum humidity conditions prevail.

The Influence of Myriapods in Soil

Myriapods play two different rôles in the soil. As carnivores they are of little evident economic significance. As herbivores many species are important in soil formation; a few attack cultivated plants and cause varying amounts of damage.

The food habits of pauropods are unknown. These myriapods are so small and appear so infrequently that almost nothing is known about them except their morphology. If morphology be accepted as a criterion upon which to judge probable food habits, then the Pauropodidae, with long, rounded bodies, long legs, and agile movements, are predators on microscopic humus animals; and the Eurupauropodidae, with depressed bodies, thickened cuticle, short legs, and slow movements are scavengers.

The long bodies, long legs, and agile movements of symphylans enable them also to prey upon microscopic humus animals. In addition, they eat soft tissues of living and dead plants. They are serious pests on plants in many greenhouses and fields, where they may occur in numbers so great that they destroy crops. In nature they do not appear in such great numbers, nor do they do any apparent damage to living plants other than minute algae and fungi. Predators, which are known to include centipedes and larvae and adults of two species of beetles, probably act as a check on the increase of the symphylan population in nature; in cultivated fields these natural enemies are generally absent.

Chilopods, with their long bodies, long legs, agile movements, and poison claws, are well-fitted to prey upon humus animals. They are known to capture and eat other chilopods, symphylans, soft-bodied insects, worms, mollusca, spiders, and occasional salamanders and lizards.

With but few exceptions, diplopods are feeders upon decaying organic matter. Among the exceptions are a few species known to be predators on humus animals; a few occasionally attack cultivated plants, but never in such great numbers or with such great economic loses as symphylans. Diplopods which obtain all of their nourishment from soil ingest large amounts of it because the nutriments in the soil available to them occur in small amounts. Sometimes they may ingest as much as two or three times their own body weight daily. Because of this, diplopods probably rank second to earthworms in soil formation, but their importance as such has not been adequately recognized. Their work is chiefly mechanical; it consists of grinding organic matter and mineral

soil and tunneling through the soil. Indirectly they also affect the soil chemically, since some chemical action takes place when the soil constituents pass through the digestive system, and their bodies, upon decomposition, contribute to the organic matter in soil.

Coville (1913) called attention to the work of diplopods in soil formation. He estimated that adults of *Spirobolus marginatus* eat 0.5 cc of leaf letter each day; the population that he found in a locality near Washington, D. C., would thus contribute to the formation of more than 2 tons of leafmold per acre annually. Heimberg (1933) and Romell (1936) reported that several species of the genus Fontaria produce significant amounts of detritus mull in some localities. Romell (1936) found that on a sunny slope in a pine-hardwood stand in the Adirondacks lumps of excrement from *Fontaria trimaculata* formed a considerable part of the 6 cm H-layer of the soil. The lumps, which were from a few millimeters to several centimeters in diameter, contained fragments of hyphae, other organic detritus, and mineral granules; their average organic matter content was 27 per cent. Berheim (1931), reported similar significant activities of European diplopods in soil formation. The amount of organic matter and soil ingested by *Orthomorpha gracilis* varied from day to day with the kind available, the temperature, the maturity of the millipedes, and with the individuals; larvae at temperatures from 29° to 31° C ingested more organic matter and soil than adults at the same temperatures or larvae and adults at lower temperatures. *Spirobolus marginatus* showed similar

variations in the amount of organic matter ingested. It is suggested that such variations are typical of soil-eating diplopods in general, and that their value as soil formers varies with the nature of the substratum, its temperature and moisture content, the species, and the maturity of the individual.

SUMMARY

1. Myriapods were referred to as Julus (=Diplopoda) and Scolopendra (=Chilopoda) from Aristotle's time until Latreille designated several genera in 1817.

2. During the eighteenth and nineteenth centuries myriapods were classified by various authors with worms, arachnids, and crustaceans, but most often with insects.

3. At the present time many authors regard myriapods as composing four distinct classes, Pauropoda, Symphyla, Diplopoda, and Symphyla?, of the Phylum Arthropoda.

4. A key is given for 96 species of myriapods that are reported to occur in North Carolina. Three species are symphylans; 45 are diplopods; and 48 are chilopods. No pauropods have been collected in the Southeastern States.

5. During 1939 and 1940 eleven species of previously undescribed myriapods were collected by the author in North Carolina. Two were symphylans, six were diplopods, and four were chilopods.

6. In the Duke Forest chilopods are more evenly distributed than diplopods. During the day chilopods are most numerous in the A_0 horizon of the soil and diplopods are most numerous in the A_1 horizon.

7. The only type of stand in the Duke Forest where myriapods do not normally occur are floodplains that are inundated

too frequently to permit litter to accumulate.

8. In the Duke Forest in October, November, and December, 1939, the greatest number of myriapods was collected from quadrats in which the moisture percentage of the oven dry-weight of the A_1 horizon of the soil at a depth of 5 to 7 cm was between 31 and 40. Quadrats in which the temperature of the A_1 horizon at a depth of 3 cm was between 12° and 14° F yielded more myriapods than any others. The average number of myriapods collected from quadrats in pine, upland hardwood, and pine-hardwood stands were about equal, while the average number collected from quadrats in bottomland hardwood forests was four times as great as from any other kind of forest stands.

9. In cultures of myriapods in the Duke Forest, between December and April specimens of *Spirobolus marginatus* showed a preference for the A_1 horizon of the soil; *Callipus lactarius* and *Polydesmus serratus* occurred most frequently in the A_0 horizon and in or under logs; *Apheloria coreacea* and *Fontaria sp.* usually occurred in the upper 3 cm of the A_1 horizon; *Orthomorpha gracilis* larvae occurred under logs, in the A_0 horizon, and as deep as 8 cm in the A_1 horizon; and *Otocryptops sexspinosus* occurred in logs, in the A_0 horizon, and as deep as 12 cm in the A_2 horizon.

10. Of the myriapods tested, *Spirobolus marginatus* was most resistant to desiccation and *Polydesmus serratus* was least resistant. *Cambala annulata*, *Callipus lactarius*, *Orthomorpha gracilis*, *Otocryptops sexspinosus*, and *Linotenia fulva* were intermediate. Death from desiccation occurred when approximately 50 per cent of the total water content of the body was lost.

11. Orthomorpha gracilis.

(a) Adults and larvae are present throughout the year in greenhouses where a temperature above 22° C is maintained and during summer and fall months in the open at Durham, North Carolina. Only larvae occur in the open during the winter and early spring months.

(b) Adults breed throughout the year in greenhouses where a temperature above 22° C is maintained.

(c) The incubation period of eggs at heated room temperatures is approximately 10 days.

(d) Larvae pass through seven stadia, which can be distinguished by differences in body size and numbers of post-cephalic somites and pairs of legs.

(e) At all stadia from the fourth through the adult females are larger and have one more pair of walking legs than males.

(f) The duration of each stadium increases successively from the first, which lasts approximately 24 hours, through the seventh, which lasts 60 or more days at heated room temperatures.

(g) The transition of larvae from one stadium to the next is accomplished by anamorphic molts, during which additional post-cephalic somites and legs are added. The second through the seventh molts take place in molting chambers constructed in soil by the larvae.

(h) The molting process consists of the following four phases: preparatory, rigidation, actual molting, and recovery. The time required for molting at heated room temperatures increases with each succeeding molt from approximately three to

six hours for the first to 20 days for the seventh. During the fourth molt the preparatory period lasts 2 days, the rigidation period 4 days, the actual molting 6 hours, and the recovery period 4 days. Larvae usually eat the exuvae during the recovery period.

(i) Five specimens passed through the seven larval stadia in from 148 to 177 days at heated room temperatures. Exposures to low temperatures lengthened the larval life.

(j) The sex ratio of 630 individuals was 3 males to 4 females.

(k) The high lethal temperature is between 39.0° and 39.5° C at relative humidities between 0 and 100 per cent when the increase in temperature is at the rate of one degree centigrade in five minutes. Quick freezing temperatures over periods longer than ten minutes are fatal.

(l) Adults and larvae of the seventh stadium died within 30 hours at humidities of 90 per cent or less; at a humidity of 100 per cent they lived until death resulted from starvation.

(m) Adults survived submersion in water from 5 to 7 days.

12. The chief factor which influences the distribution of myriapods is the presence of moist humus.

13. Many diplopods are important in soil formation by reason of their grinding and mixing soil and organic matter.

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APPENDIX

Figures 1, 2, 3

Explanation of Figures 1, 2, and 3

Figure 1. Diagram showing the ancestry and relationship of myriapods, after Tillyard (1936).

Figure 2. Diagram showing the ancestry and relationship of myriapods, after Verhoeff (1925).

Figure 3. Diagram showing the ancestry and relationship of myriapods, after Snodgrass (1938).

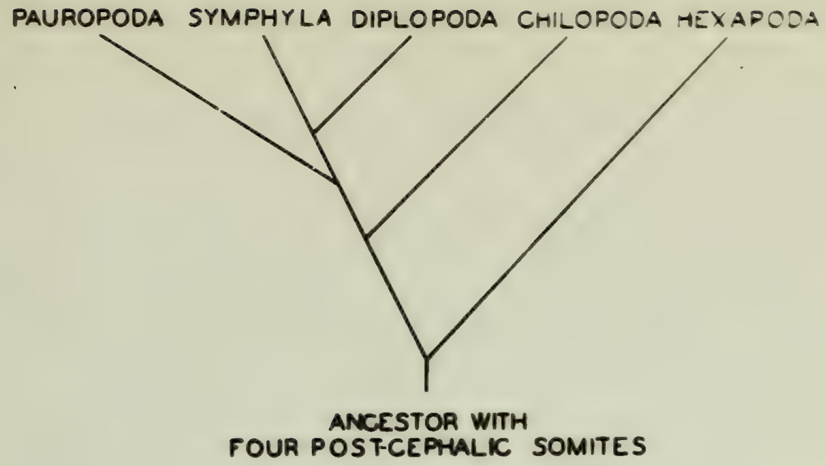


FIG. 1

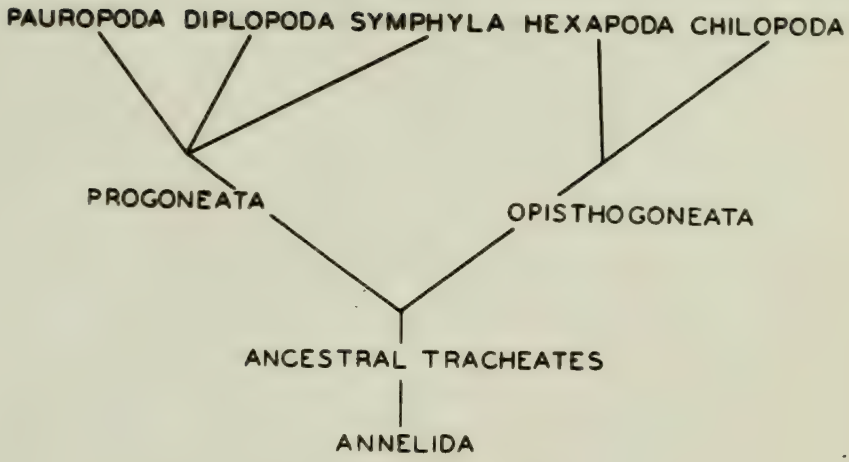


FIG. 2

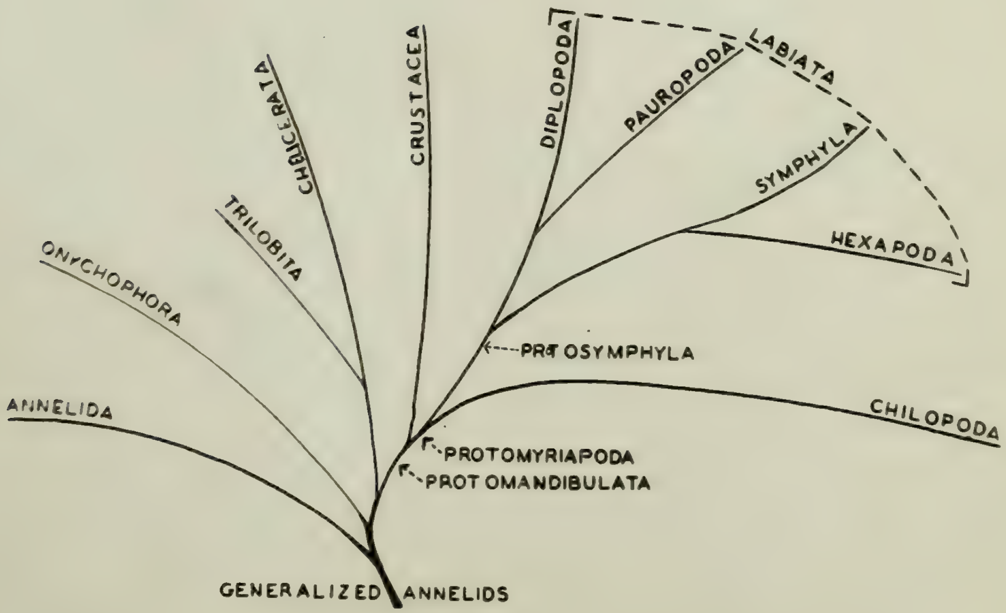


FIG. 3

Figures 4 through 20

Explanation of Figures 4 through 20

Figure 4. *Euryurus erythropygus* (from Williams and Hefner). Lateral view of right gonopod.

Figure 5. *Scytonotus granulatus* (from Williams and Hefner). Median view of right gonopod.

Figure 6. *Brachydesmus dux*. Median view of left gonopod.

Figure 7. *Polydesmus serratus* (from Williams and Hefner). Median view of left gonopod.

Figure 8. *Leptodesmus hispidipes* (after Wood). Gonopod.

Figure 9. *Zinaria virginiensis* (from Williams and Hefner). Posterior view of right gonopod.

Figure 10. *Apheloria coriacea* (from Williams and Hefner). Posterior view of right gonopod.

Figure 11. *Apheloria aspila* (from Chamberlin 1939). Submesal view of right gonopod.

Figure 12. *Apheloria tigana* (from Chamberlin 1939). Submesal view of right gonopod.

Figure 13. *Apheloria unaka* (from Chamberlin 1939). Subcephalic view of right gonopod.

Figure 14. *Apheloria waccamana*. Lateral view of gonopod.

Figure 15. *Sigiria scorpio* (from Chamberlin 1939). Caudoventral view of right gonopod.

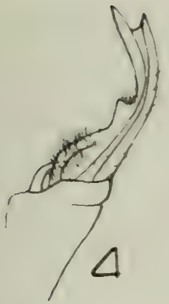
Figure 16. *Sigmoria munda* (from Chamberlin 1939). Caudal view of right gonopod.

Figure 17. *Sigmoria munda* (from Chamberlin 1939). Ectal view of spur of principal blade.

Figure 18. *Sigmoria abberans* (from Chamberlin 1939). Anteromesal view of left gonopod.

Figure 19. *Sigmoria conclusa* (from Chamberlin 1939). Subcaudal view of right gonopod.

Figure 20. *Sigmoria conclusa* (from Chamberlin 1939). Caudal view of right gonopod.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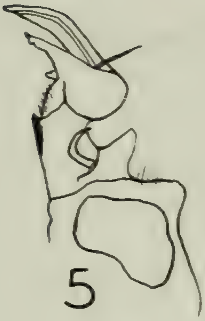
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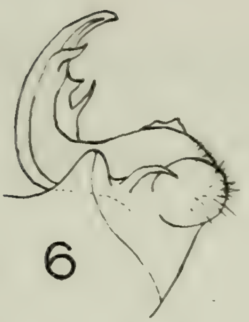
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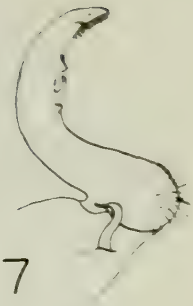
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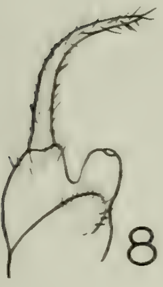
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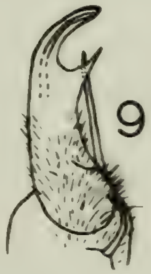
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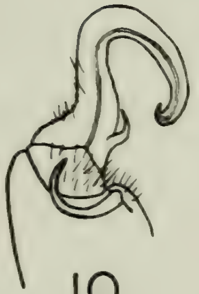
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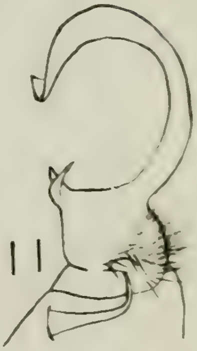
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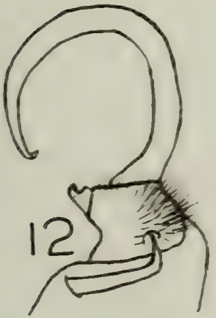
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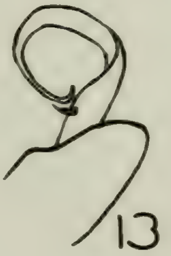
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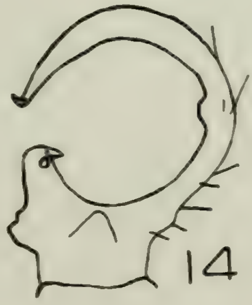
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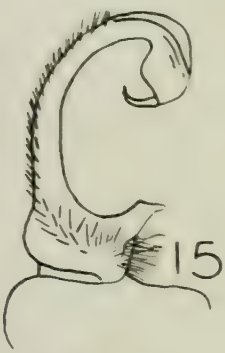
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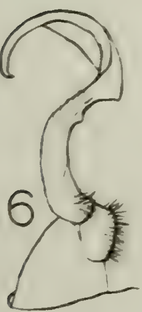
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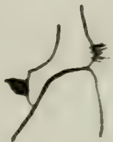
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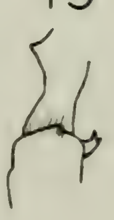
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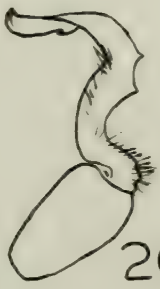
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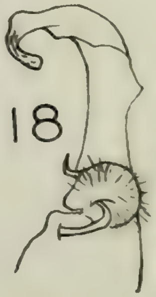
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Figures 21 through 38

Explanation of Figures 21 through 38

Figure 21. *Sigmoria divergens* (from Chamberlin 1939). Subcaudal view of right gonopod.

Figure 22. *Sigmoria divergens* (from Chamberlin 1939). Ectal view of left gonopod.

Figure 23. *Sigmoria mariona* (from Chamberlin 1939). Subcaudal view of right gonopod.

Figure 24. *Sigmoria mariona* (from Chamberlin 1939). Ectal view of base of principal blade of gonopod.

Figure 25. *Mimuloria ducilla* (from Chamberlin 1939). Right gonopod.

Figure 26. *Aporiaria carolina* (from Chamberlin 1939). Right gonopod.

Figure 27. *Aporiaria geniculata* (from Chamberlin 1939). Right gonopod.

Figure 28. *Parjulus canadensis* (from Williams and Hefner). Cephalic view of gonopods.

Figure 29. *Parajulus impressus* (from Williams and Hefner). Cephalic view of gonopods.

Figure 30. *Parajulus pennsylvanicus* (from Williams and Hefner). Cephalic view of gonopods.

Figure 31. Diagram of the labrum of *Agathothus gracilis*; the relatively large median piece is armed with a fringe of teeth or spines, and the small lateral pieces are unarmed (from Chamberlin 1912).

Figure 32. Diagram of the labrum of *Arenophilus watsingus*, which consists of a relatively small median piece and large lateral pieces, which are armed on the free edge with many spinescent processes (from Chamberlin 1912).

Figure 33. *Agathothus gracilis* (from Chamberlin 1912). a. Dorsal view of anterior portion. b. One prehensor with part of prosternum.

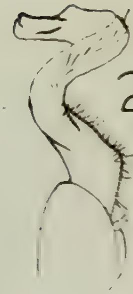
Figure 34. Diagram of one prehensor with part of prosternum; the toothed claw is characteristic of members of the genus Linotenia.

Figure 35. *Geophilus rubens*. One prehensor with part of prosternum.

Figure 36. *Arenophilus watsingus* (from Chamberlin 1912). Ventral view of anterior portion.

Figure 37. *Lithobius foricatus* (from Attems 1930). Ventral view of posterior portion of female. A-anal leg; C-coxal pore in coxa of anal leg; G-gonopod; P-ventral plate of pregenital somite; S-ventral plate of last leg bearing somite.

Figure 38. Diagram of Lithobiid leg (from Williams and Hefner). In the formula beneath the upper row of figures designates the dorsal spines and the lower row the ventral spines on the five leg segments. C-Coxa; F-femur; PF-pre-femur; T-trochanter; TI-tibia; T1 and T2-first and second tarsi.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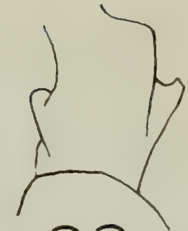
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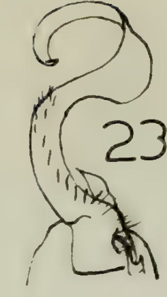
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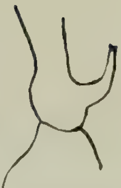
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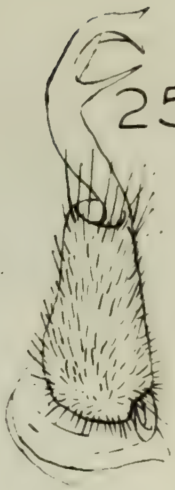
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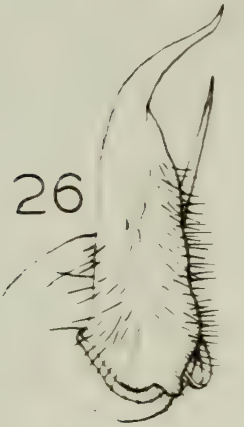
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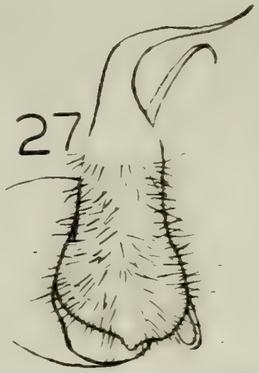
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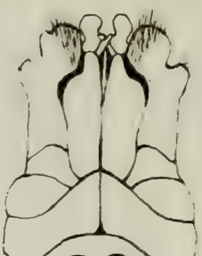
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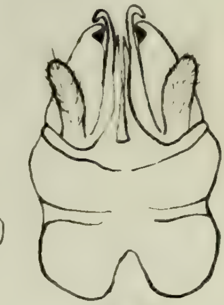
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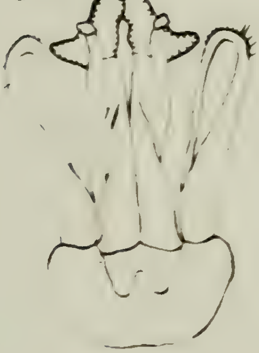

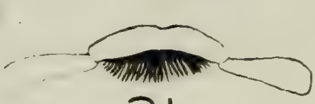
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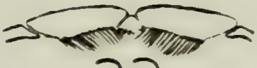
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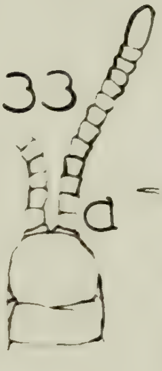

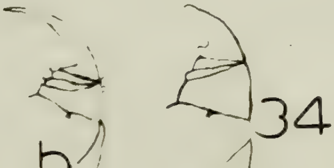

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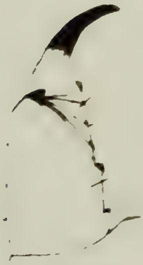
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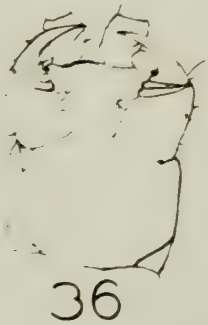
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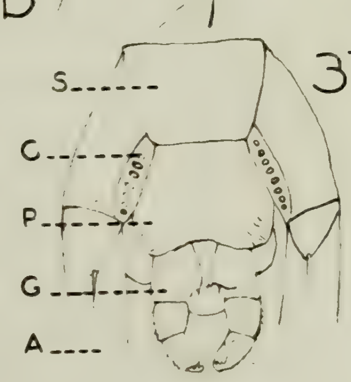

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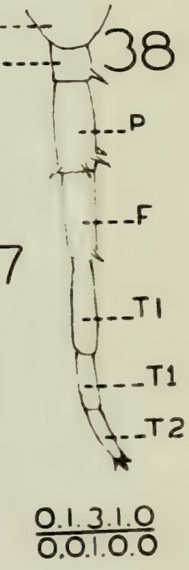

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Figures 39 and 40

Explanation of Figures 39 and 40

Figure 39. Graphs to show the numbers of myriapods collected in relation to the temperature of the A_1 horizon of the soil at a depth of 3 cm.

Figure 40. Graphs to show the numbers of myriapods collected in relation to the moisture percentage of the oven-dry weight of the A_1 horizon of the soil at a depth of 5 - 7 cm.

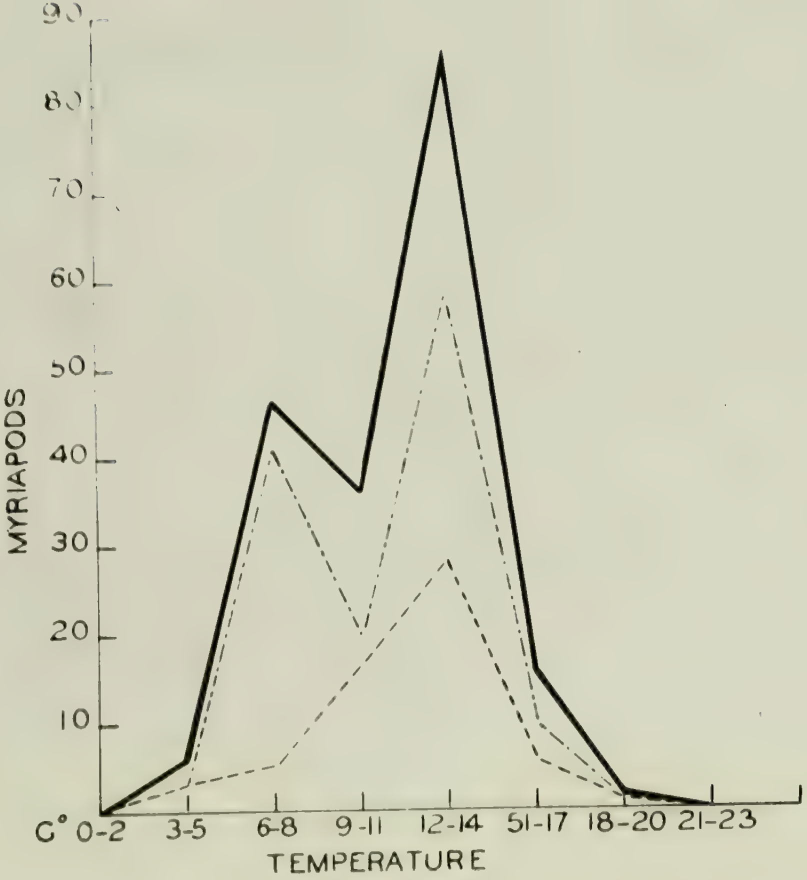
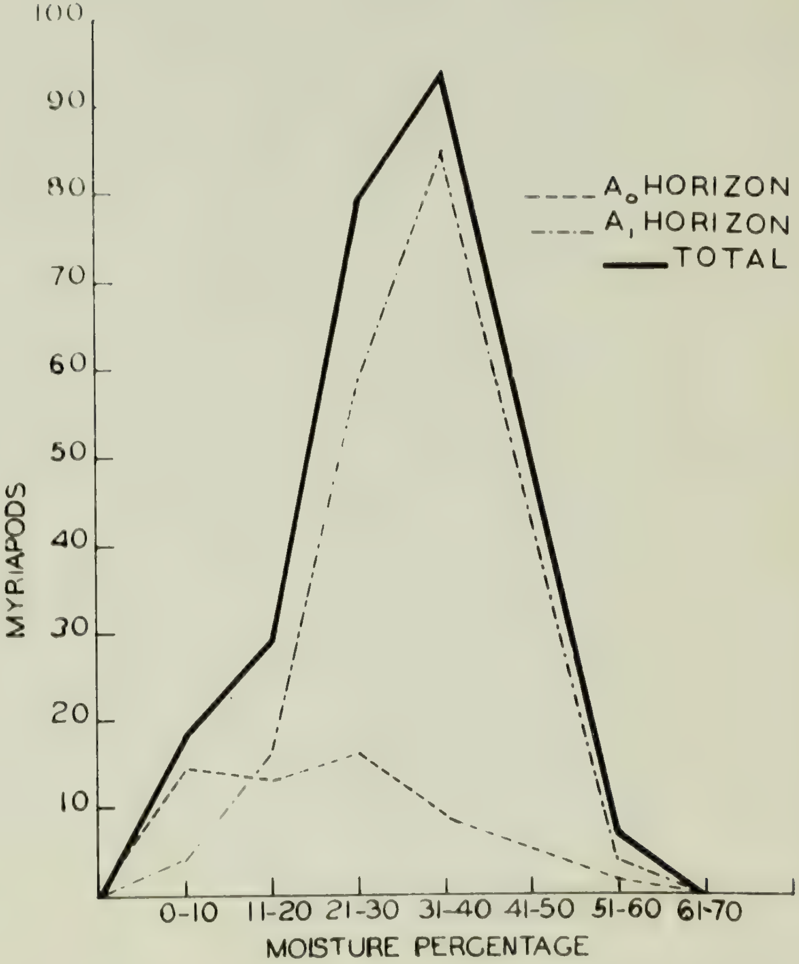

90
80
70
60
50
40
30
20
10
MYRIAPODS
C° 0-2
3-5
6-8
9-11
12-14
51-17
18-20
21-23
TEMPERATURE

FIG. 39


100
90
80
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30
20
10
MYRIAPODS
0-10
11-20
21-30
31-40
41-50
51-60
61-70
MOISTURE PERCENTAGE
A₀ HORIZON
A₁ HORIZON
TOTAL

FIG. 40

Figures 41, 42, and 43

Explanation of Figures 41, 42, and 43

Figure 41. Graphs to show the numerical distribution of myriapods in the four principal cover types in the Duke Forest. The average number of myriapods per quadrat was taken from all of the quadrats in stands of a particular cover type. There were ten quadrats in pine-hardwood (P-H) stands, five in upland hardwood stands (UH), four in pine (P) stands, and three in bottomland hardwood (BH) stands.

Figure 42. Graphs to show the average numbers of chilopods and diplopods per quadrat in the A_0 horizon, or litter, of the soil in the four principal cover types in the Duke Forest. C, chilopods; D, Diplopods; T, total number of chilopods and diplopods; other letters refer to the forest stands that were listed above in the explanation of Figure 41.

Figure 43. Graphs to show the average numbers of chilopods and diplopods per quadrat in the upper 8 cm of the A_1 horizon of the soil in the four principal cover types in the Duke Forest. The letters refer to the same myriapods and forest stands that were listed above in the explanations of Figures 41 and 42.

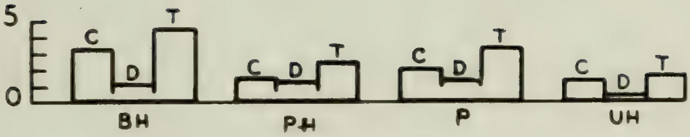

FIG.42

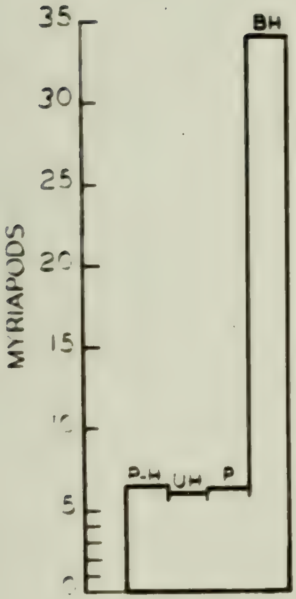

FIG.41

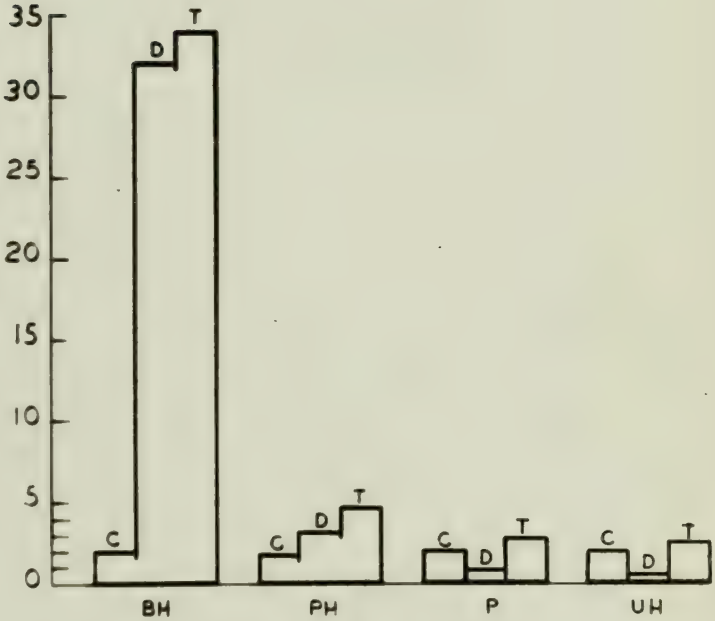

FIG.43

Figure 44

Explanation of Figure 44

Figure 44. A map showing the distribution of *Orthomorpha gracilis*.

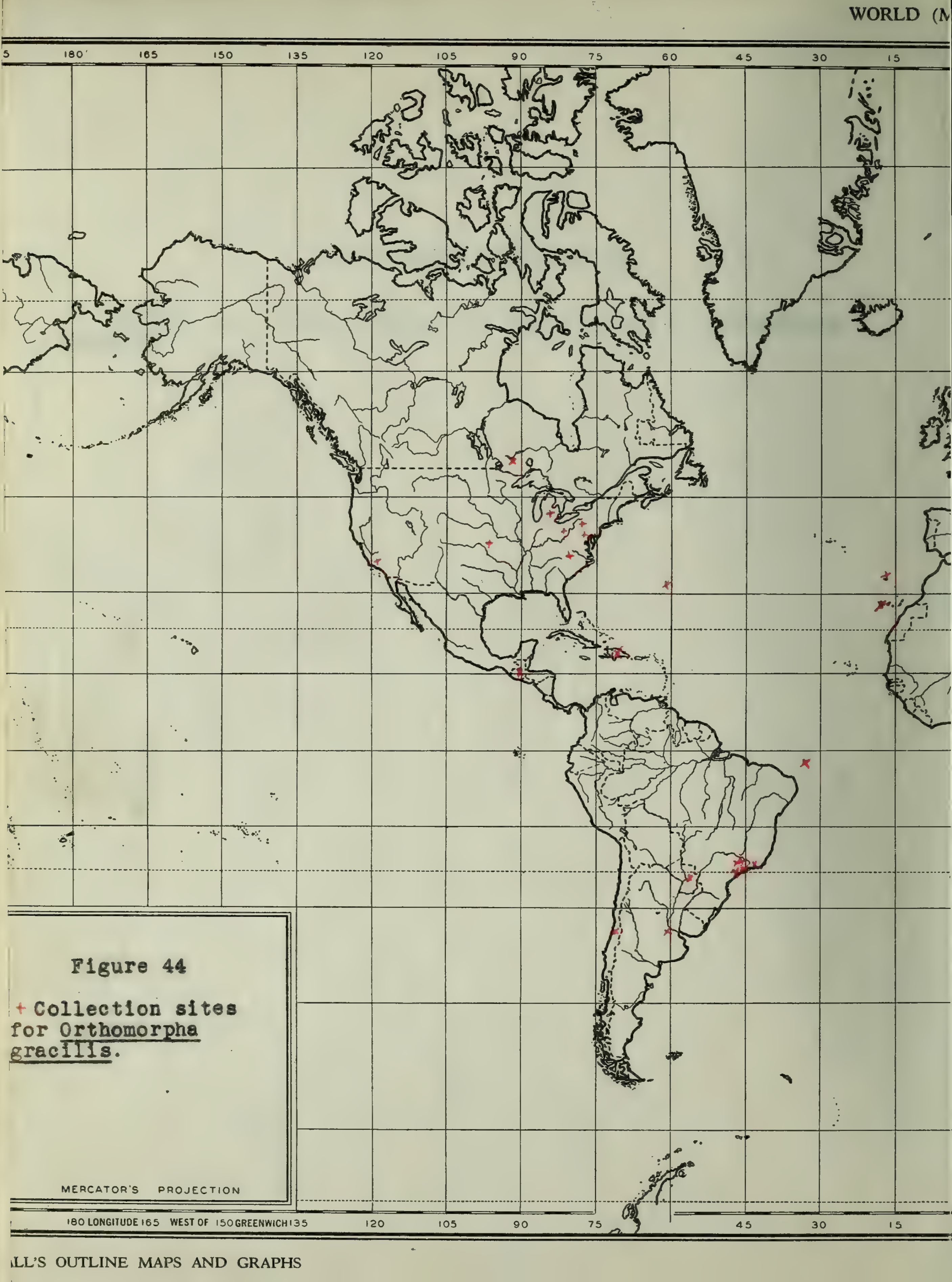

Figure 44

+ Collection sites for *Orthomorpha gracilis*.

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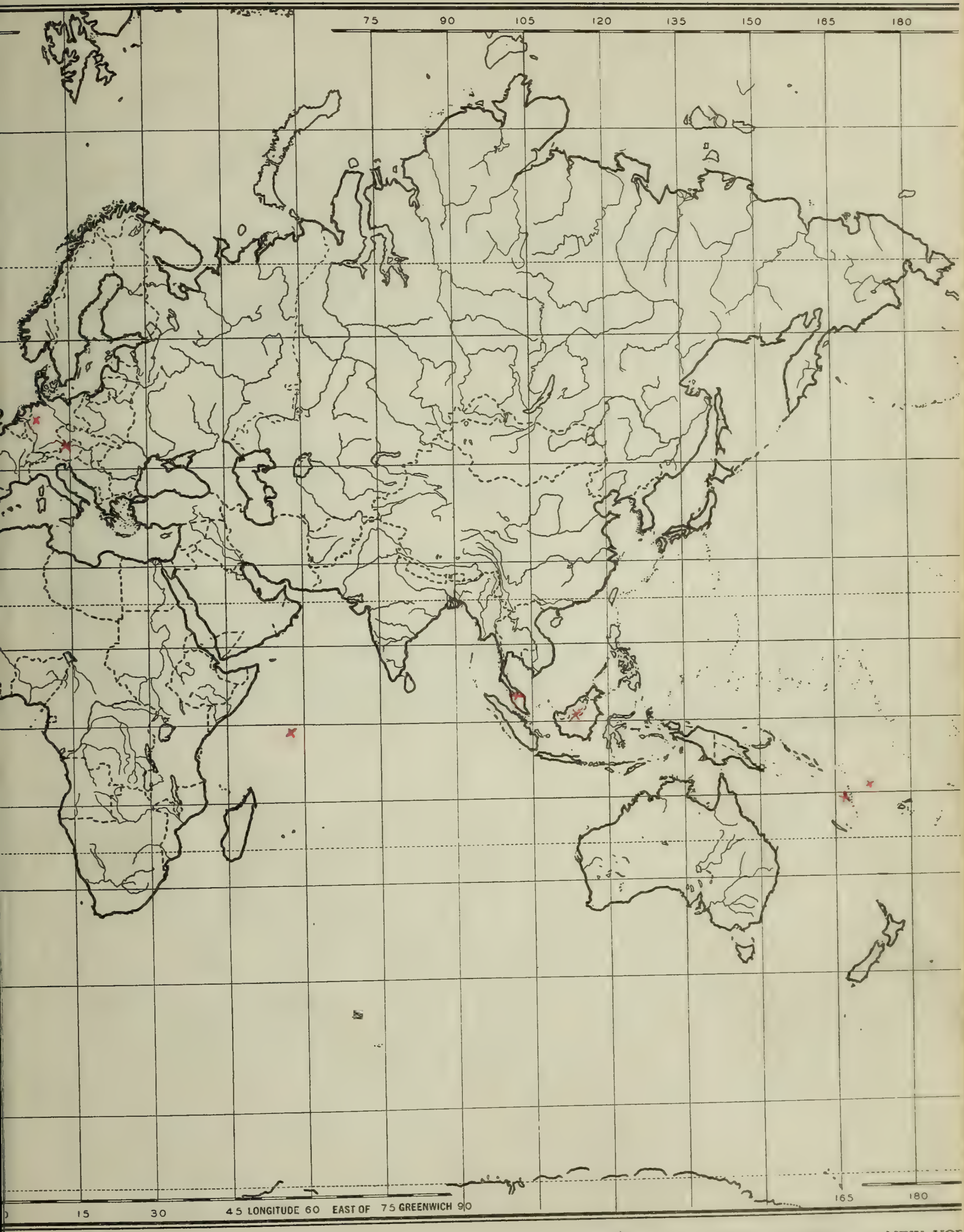

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Explanation of Figures 45 through 51

Figure 45. *Orthomorpha gracilis*. Lateral view of right gonopod (x72).

Figure 46. *Orthomorpha gracilis*. Structure of the gnathochilarium; C-cards; G-glossa; L-lamella lingualis; Lo-lobes on end of stipe; M-mentum; P-paraglossa; S-stipes; St-sternum of first post-cephalic somite (x72).

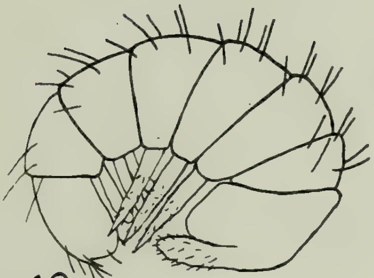
Figure 47. *Orthomorpha gracilis*. Sixth, seventh, and eighth articles of antenna; S-sensory spine (x72).

Figure 48. *Orthomorpha gracilis*. Structure of a walking leg; C-claw; Co-coxa; F-femur; Po-postfemur; Pr-prefemur; T-tarsus; Ti-tibia (x36).

Figure 49. *Orthomorpha gracilis*. A larva of the first stadium (x72).

Figure 50. *Orthomorpha gracilis*. A larva of the second stadium (x72).

Figure 51. *Orthomorpha gracilis*. Structure of a premandible; B-basal plate; L-pectinate lamellae; M-middle piece; P-rasping plates; T-main tooth; Ti-inner tooth.



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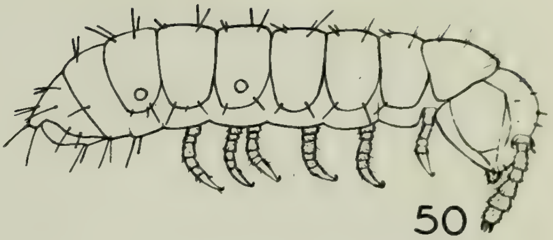

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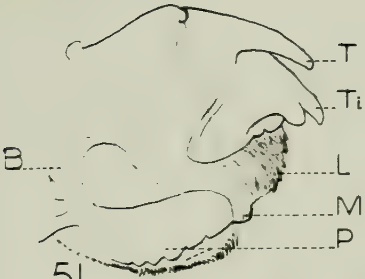

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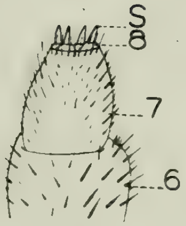

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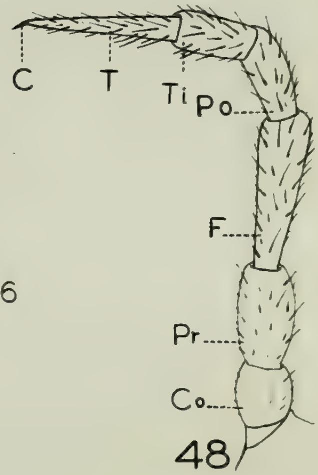

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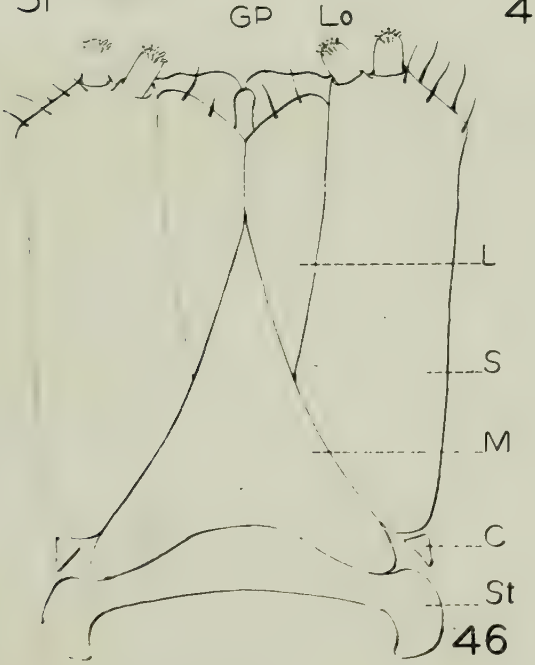

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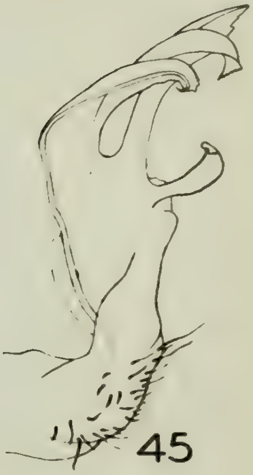

45

Table 1. The Numbers and Species of Myriapods Collected from Twenty-three Quadrats 1.5 Meter by 1.5 Meter in Area. There were no myriapods in Quadrats 3 and 5.

Quadrats	1	2	4	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Myriapods in A_0 Horizon																					
Geophilomorpha	-	-	-	-	-	-	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-
Lithobiomorpha	2	-	-	-	1	-	-	-	-	-	-	1	-	1	3	2	-	-	-	-	-
Otocryptops sexspinosus	-	1	-	-	3	-	-	1	-	-	-	8	8	5	-	1	-	-	-	-	-
Theatops posticus	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	2	-	-	-	-
Cryptops hyalinus	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Juloidea	-	-	1	-	-	-	-	-	-	2	-	4	-	2	2	-	-	3	-	-	-
Cambala annulata	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Cleidogona caesioannulata	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
Craspedosmidae	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Callipus lactarius	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Polydesmus serratus	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Scynotus granulatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Total in A_0 Horizon in Each Quadrat	4	2	1	-	4	-	1	1	-	8	-	14	9	10	5	3	3	3	-	-	-
Myriapods in A_1 Horizon																					
Symphyla	-	-	1	-	-	-	-	-	-	-	-	-	-	3	1	1	4	-	-	-	1
Geophilomorpha	5	-	-	1	1	-	1	-	-	4	-	1	1	4	1	2	5	-	-	-	3
Lithobiomorpha	-	-	-	-	-	-	-	-	1	-	-	-	-	-	2	2	-	-	-	-	2
Otocrypyops sexspinosus	1	-	-	-	-	-	-	-	1	-	-	2	-	-	-	-	-	-	-	-	-
Theatops posticus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Juloidea	-	-	-	-	-	-	1	-	-	-	-	-	-	-	2	-	-	-	-	-	-
Cleidogona caesioannulata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Spirobolus marginata	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	1	1	-
Fontariidae	4	-	-	-	43	2	-	-	-	-	2	-	-	20	28	-	-	-	-	-	-
Total in A_1 Horizon in Each Quadrat	10	-	1	-	44	3	2	-	2	4	2	4	1	27	35	5	9	-	2	1	6
Total in Each Quadrat	14	2	2	1	48	3	3	1	2	12	2	18	10	37	40	8	12	3	2	1	6

Table 2

Percentage of Total Water Content Lost by Six Specimens of *Spirobolus marginatus* during Twenty-four Hour Periods at Various Humidities and Temperatures from 29° to 31° C

Original Weight in Grams	24 Hour Period	Weight after Exposure	Percentage of Water Lost	Condition
		Humidity 96 Per Cent		
1.6300	1	1.6291	.08	alive
	2	1.5985	2.63	"
	3	1.4851	9.75	"
	4	1.4329	4.48	"
	5	1.3813	4.44	"
	6	1.3305	4.37	"
	7	1.2834	4.05	"
	8	1.2532	2.60	"
	9	1.2270	2.25	"
	10	1.2012	2.22	"
	11	1.1845	1.44	"
	12	1.1716	1.11	"
	13	1.1550	1.43	"
	14	1.1252	2.56	"
	15	1.0883	3.17	"
	16	1.0389	4.24	"
	17	0.7227	27.17	dead
		Humidity 80 Per Cent		
3.1068	1	2.8372	12.27	alive
	2	2.6420	8.88	"
	3	2.2296	18.77	"
	4	2.0530	8.04	"
	5	1.8810	7.82	"
	6	1.7372	6.54	dead
		Humidity 60 Per Cent		
4.9450	1	4.4510	12.92	alive
	2	4.0483	10.55	"
	3	3.8170	6.06	"
	4	3.5790	6.23	"
	5	3.3052	7.17	"
	6	3.1430	4.25	"
	7	2.8140	8.62	"
	8	2.6831	3.44	"
	9	2.5529	3.41	"
	10	2.4062	3.84	"
	11	2.1910	5.64	dead

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Table 2 (continued)

Humidity 60 Per Cent

2.9212	1	2.6072	15.89	alive
	2	2.4255	9.29	"
	3	2.2192	10.44	"
	4	2.0973	6.17	"
	5	1.9622	6.83	"
	6	1.8460	5.38	dead
0.2901	1	0.2170	33.68	alive
	2	0.1886	13.07	dead

Humidity 15 Per Cent

7.1032	1	5.5798	29.68	alive
	2	5.0640	10.05	"
	3	4.5156	10.68	"
	4	4.1675	6.78	"
	5	3.7701	7.74	"
	6	3.4320	6.59	dead

Table 3

Percentage of Total Water Content Lost by Five Specimens of Cambala annulata during Twenty-four Hour Periods at Various Humidities and Temperatures from 29° to 31° C

Original Weight in Grams	24 Hour Period	Weight after Exposure	Percentage of Water Lost	Condition
		Humidity 96 Per Cent		
0.2114	1	0.1934	12.6	alive
	2	0.1737	13.7	"
	3	0.1627	7.7	"
	4	0.1535	6.4	"
	5	0.1459	4.9	"
	6	0.1363	6.3	dead
		Humidity 88 Per Cent		
0.4169	1	0.3355	29.0	alive
	2	0.3089	9.5	"
	3	0.2867	7.9	"
	4	0.2677	6.8	"
	5	0.2507	6.1	dead
		Humidity 80 Per Cent		
0.3095	1	0.2473	33.3	alive
	2	0.2199	14.7	"
	3	0.1874	17.4	dead
		Humidity 60 Per Cent		
0.2914	1	0.2458	22.1	alive
	2	0.2113	16.7	"
	3	0.1709	19.6	dead
		Humidity 15 Per Cent		
0.2147	1	0.1814	25.8	alive
	2	0.1365	34.8	dead

Table 4

Percentage of Total Water Content Lost by Four Specimens of *Callipus lactarius* during Twenty-four Hour Periods at Various Humidities and Temperatures from 29° to 31° C

Original Weight in Grams	24 Hour Period	Weight after Exposure	Percentage of Water Lost	Condition
		Humidity 96 Per Cent		
0.1712	1	0.1459	25.2	alive
	2	0.1300	15.9	"
	3	0.1149	15.1	dead
		Humidity 88 Per Cent		
0.2859	1	0.2373	27.0	alive
	2	0.2003	20.5	"
	3	0.1600	22.4	dead
		Humidity 80 Per Cent		
0.3230	1	0.2200	48.8	alive
	2	0.1485	33.9	dead
		Humidity 60 Per Cent		
0.3395	1	0.2365	45.9	alive
	2	0.1780	26.1	dead

Table 5

Percentage of Total Water Content Lost by Six Specimens of *Orthomorpha gracilis* during Twenty-four Hour Periods at Various Humidities and Temperatures from 29° to 31° C

Original Weight in Grams	24 Hour Period	Weight after Exposure	Percentage of Water Lost	Condition
		Humidity 96 Per Cent		
0.0575	1	0.0545	8.1	alive
	2	0.0535	2.9	"
	3	0.0401	38.8	dead
		Humidity 88 Per Cent		
0.0630	1	0. 0468	43.0	dead
		Humidity 80 Per Cent		
0.0700	1	0.1549	27.9	alive
	2	0.0411	23.7	dead
		Humidity 60 Per Cent		
0.0905	1	0.0660	45.0	alive
	2	0.0395	48.7	dead
		Humidity 15 Per Cent		
0.0228	1	0.0078	89.8	dead
		Humidity 0 Per Cent		
0.0375	1	0.0190	90.2	dead

Table 6

Percentage of Total Water Content Lost by Five Specimens of *Polydesmus serratus* during Twenty-four Hour Periods at Various Humidities and Temperatures from 29° to 31° C

Original Weight in Grams	24 Hour Period	Weight after Exposure	Percentage of Water Lost	Condition
		Humidity 96 Per Cent		
0.1420	1	0.1226	18.9	alive
	2	0.1661	55.0	dead
		Humidity 88 Per Cent		
0.1772	1	0.1066	55.2	dead
		Humidity 80 Per Cent		
0.1893	1	0.1893	52.2	dead
		Humidity 60 Per Cent		
0.1762	1	0.1082	55.8	dead
		Humidity 15 Per Cent		
0.1875	1	0.0873	77.5	dead

Table 7

Percentage of Total Water Content Lost by Three Specimens of *Otocryptops sexspinosus* during Twenty-four Hour Periods at Various Humidities and Temperatures from 29° to 31° C

Original Weight in Grams	24 Hour Period	Weight after Exposure	Percentage of Water Lost	Condition
Humidity 88 Per Cent				
0.7616	1	0.6922	14.7	alive
	2	0.6415	10.7	"
	3	0.5915	10.6	"
	4	0.5335	12.0	dead
Humidity 80 Per Cent				
0.8848	1	0.8164	15.9	alive
	2	0.7105	16.4	"
	3	0.5906	18.6	"
	4	0.4645	19.5	dead
Humidity 60 Per Cent				
0.4205	1	0.3495	21.0	alive
	2	0.2786	21.0	"
	3	0.1886	26.7	dead

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Table 8

Percentage of Total Water Content Lost by Two Specimens of _Linotenia fulva_ during Twenty-four Hour Periods at at Various Humidities and Temperatures from 29° to 31° C

Original Weight in Grams	24 Hour Period	Weight after Exposure	Percentage of Water Lost	Condition
		Humidity 80 Per Cent		
0.0417	1	0.0342	22.1	alive
	2	0.0250	27.1	"
	3	0.0157	29.4	dead
		Humidity 60 Per Cent		
0.0700	1	0.0486	40.2	alive
	2	0.0277	39.2	dead

Table 9

The Numbers of Each Sex of *Orthomorpha gracilis* in Collections Made Jan. 23, Feb. 6, and Feb. 27, 1940

	Adult		Seventh Stadium		Sixth Stadium	
	Male	Fem.	Male	Fem.	Male	Fem.
	13	16	43	52	10	17
	11	20	14	20	-	-
	63	100	73	83	46	48
Total	87	136	130	155	56	65

Table 10

Number of Post-cephalic Somites, Number of Pairs of Legs, Location of Legs and Anus (A), and Mean Length of Ten Individuals of Both Sexes of Each Stadium in the Life History of
Orthomorpha gracilis

Stadium	No. Post-cephalic Somites	No. Pairs Legs	Pairs of Legs on Each Post-cephalic Somite																				Length in Mm.
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
I	7	3	0	1	1	1	0	0	A														0.51
II	9	6	0	1	1	1	2	1	0	0	A												1.55
III	12	11	0	1	1	1	2	2	2	2	0	0	0	A									3.60
IV	15	16	0	1	1	1	2	2	1	2	2	2	2	0	0	0	A						4.15
		17	0	1	1	1	2	2	2	2	2	2	2	0	0	0	A						4.61
V	17	22	0	1	1	1	2	2	1	2	2	2	2	2	2	2	0	0	A				4.82
		23	0	1	1	1	2	2	2	2	2	2	2	2	2	2	0	0	A				5.67
VI	18	26	0	1	1	1	2	2	1	2	2	2	2	2	2	2	2	2	0	A			7.41
		27	0	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	0	A			7.80
VII	19	28	0	1	1	1	2	2	1	2	2	2	2	2	2	2	2	2	2	0	A		12.43
		29	0	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	0	A		13.20
VIII	20	30	0	1	1	1	2	2	1	2	2	2	2	2	2	2	2	2	2	2	0	A	19.25
		31	0	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0	A	20.82

Table 11

The Percentage of Sixth Instar Larvae of *Orthomorpha gracilis* that Molted within Forty Days under Varied Substrata and Temperature Conditions

	29°-31° C		12°-20° C		3.5° C		Summary for Each Substratum	
Substratum	No. Larvae	Percentage Molted	No. Larvae	Percentage Molted	No. Larvae	Percentage Molted	No. Larvae	Percentage Molted
Loam	20	40	30	50	10	0	60	38.3
Sand	10	0	10	30	10	0	30	10.0
Leaf Mold	30	33	20	60	10	0	60	36.6
Summary for Each Temperature	60	30.0	60	50.0	30	0.0		

Table 12

The Percentage of Body Weight of Faeces from Ten Seventh Instar Larvae and Ten Adults of *Orthomorpha gracilis* that Fed Twenty-four Hours on Manure, Loam, and Leafmold under Temperatures from 29° to 31° C and from 12° to 20° C

Food	Seventh Instar Larvae		Adult Millipedes		Mean Percentage of Weight of Faeces
	29°-31° C	12°-20° C	29°-31° C	12°-20° C	
Manure	55.2	97.5	64.37	27.3	60.7
Leafmold	131.2	48.2	38.7	43.1	65.4
Loam	92.4	12.6	39.1	37.9	45.5
Mean Percentage of Weight of Faeces	92.9	52.8	47.4	36.1	

CURRICULUM VITAE

The author was born at Trenton, Tennessee, December 8, 1910. Colleges and universities attended were Stephen F. Austin State Teachers College, 1927-1928; The College of the Ozarks, 1928-1931; the University of Arkansas, 1936-1937; and Duke University, 1937-1940. The B. S. degree was received from The College of the Ozarks in 1931 and the M. A. degree from the University of Arkansas in 1937. Appointments were held as Scholar in Zoology at the University of Arkansas, 1936-1937; Assistant in Zoology at Duke University, 1937-1939; and Fellow in Zoology at Duke University, 1939-1940. The following articles have been published:

1938. (with David Causey) Microscopic masons. Ed. Focus 9:19-21.

1938. Key to the common aquatic and emergent plants of Reelfoot Lake. Jour. Tenn. Acad. Sci. 13:120-125.

1938. Some notes on the Protozoa of Reelfoot Lake. Ibid. 13: 137-159.

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